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LIFE HISTORY AND MICROHABITAT DISTRIBUTION OF MIDGES (DIPTERA: CHIRONOMIDAE) INHABITING A BROWN-WATER STREAM OF CENTRAL ALBERTA, CANADA

BY

©

HANS BOERGER

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Life History and Microhabitat Distribution of Midges (Diptera: Chironomidae) Inhabitating a Brown-water Stream of Central Alberta, Canada", submitted by Hans Boerger in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Supervisor

W. G. Evans

Fred C. Zwickel

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Date 11 October 1978

ABSTRACT

One hundred twelve species of Chironomidae were found in emergence traps placed in a 150-m stretch of the Bigoray River, a slow-flowing, brown-water stream of central Alberta, Canada. Tanypodinae, Orthocladiinae, Chironomini and Tanytarsini made up 18%, 43%, 20% and 19% respectively, based on number of species, and 20%, 24%, 13% and 43% based on number of individuals. Yearly emergence was 19.3×10^3 chironomids/m^2. Orthocladiinae emerged in spring and fall while Tanypodinae and Chironomini emerged in summer. Peak emergence of Tanytarsini occurred after that of Orthocladiinae in the spring but before that of Orthocladiinae in the autumn. Emergence periods of individual species averaged 67 days (range 15-122 days). Emergence graphs were either unimodal (single emergence phase), bimodal (two phases) or trimodal (three phases). The phase length increased throughout the season. Average ratio of males to females was 0.8 and decreased from the beginning to the end of an emergence phase. Of the 32 species examined, 11 were univoltine, 15 were bivoltine and 6 were trivoltine. Overwintering occurred primarily as third instar larvae. Density of larvae on bottom sediment averaged $19.9 \times 10^3/m^2$, and was lowest in June and highest in March. Average densities of larvae on Sparganium, Potamogeton, Hippuris, moss, filamentous algae and sponge was 93, 171, 466, 978, 351 and 32 larvae/gm dry weight of substrate, respectively. Mean density on wood was 0.9 larvae/ cm^2. The preferred habitat of Tanypodinae and Chironomini was sediment. Orthocladiinae preferred *Sparganium*, moss and filamentous algae, and Tanytarsini preferred *Potamogeton*. Most species showed a preference for only one of the nine microhabitats. *Paramerina fragilis* was the only habitat specialist. Temporal and spatial overlap between congeneric species and between species belonging to different trophic levels was higher than between non-congeneric species and species belonging to the same trophic level. Pairs of species with high temporal overlap also had high spatial overlap. The possibility that the low temporal and spatial overlap is the result of interspecific competition is discussed.

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Thanks are also due to Dr. O.A. Saether, Museum of Zoology, University of Bergen, for assisting me with my initial attempts at chironomid taxonomy while I was visiting the Freshwater Institute, Winnipeg, and for verifying my identifications of Orthocladiinae. Dr. D.R. Oliver, Biosystematic Institute, Agriculture Canada, Ottawa, I would like to thank for making my trip to Ottawa a rewarding one as well as a pleasant one, and for verifying the identification of the Orthocladiinae and Chironomini. Dr. S.S. Roback, Academy of Natural Sciences of Philadelphia, verified my Tanytarsini; Dr. A.R. Saponis, Laboratory of Aquatic Entomology, Florida Agricultural and Mechanical University, verified my *Orthocladius*; and Dr. J.E. Sublette, Eastern New Mexico University, Portales, verified my Tanytarsini. To all these specialists I am very grateful.

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I would also like to thank the Boreal Institute, University of Alberta, for providing a grant to cover the cost of the field work in 1973. The study was also supported through a National Research Council scholarship, and through National Research Council grants to Dr. H.F. Clifford.

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I INTRODUCTION

This thesis deals with the ecology of the Chironomidae occurring in the Bigoray River, a small, slow-flowing, brown-water stream of central Alberta. Although such streams are common in boreal regions, they have been little studied, partly because of the following reasons: 1) the streams are covered with ice for five or more months; 2) dense populations of biting flies hinder field work in the summer; and 3) few roads are built through the areas of muskeg (flat, poorly-drained terrain covered with organic soils to a depth of 30 cm or more) in which these streams occur most frequently.

With the increased rate of northern development, it is important that these streams be studied while still in their natural state. Such baseline studies are needed to assess the impact of future man-made perturbations. This led Dr. Hugh F. Clifford, University of Alberta, to initiate a long-term study of the Bigoray River. This stream was chosen because it was representative of other brown-water streams, it was located only 100 km from the University of Alberta campus, it was readily accessible by an all-weather road, and it has received little disturbance by human activity.

Although considerable information had already been collected on the stream by the time this study was started (Clifford 1969, Hayden 1971, Bond 1972), no work had been done on the Chironomidae. Such omission or only superficial treatment of the Chironomidae is typical of many stream studies (Hynes 1970), even though this group has been shown to be abundant both in number of species as well as number of individuals in many aquatic habitats (Thienemann 1954, Hamilton 1965, Reiss 1968, Lehmann 1971, Lindegaard-Peterson 1972). The paucity of information on the chironomid component of stream benthos is due in part to the small size of the larvae, which necessitates special sampling techniques. Another reason is that identification of larvae to species requires their association, usually through rearing in the laboratory, with the male adult, the only life stage for which there are identification keys to species.

There was little information on Alberta chironomids at the start of my project. Strickland (1946) listed 38 species in his check lists of Alberta Diptera. Saether (1969) had recorded 24 additional species from the Waterton area of south-western Alberta. Rosenberg (1973) identified some chironomids to species as part of a study on the effect of insecticides on a pond near Edmonton. The nearest localities where chironomids had been studied in some detail were a coastal lake and stream in British Columbia (Hamilton 1965, Mundie 1971), a high mountain stream in Colorado (Saether 1970) and a lake in northern Saskatchewan (Mundie 1959).

Because there was so little information on the chironomid fauna of Alberta, I decided that a general descriptive study of the whole chironomid community of a representative stretch of the Bigoray River would be more useful and also more feasible at this stage than a more detailed experimental study of one or a few of the more common species. I decided to analyze three community parameters: 1) species composition and relative abundance of the species; 2) phenology of the different larval instars and of adult emergence; and 3) distribution of larvae in the various microhabitats found in the study area. These three parameters had been analyzed for other aquatic insects; thus allowing my results to be related to other studies. The last two parameters would also allow me to calculate temporal and spatial separation between species. These two processes have been shown to decrease competition among coexisting species and are therefore important in the structuring of communities (Collier et al. 1973, Cody 1974). Data on temporal and spatial separation can also be used to discuss questions such as:

1) What is the relative importance of temporal and spatial separation?
2) What is the relationship between temporal and spatial separation? If two species have a high degree of temporal separation, will they have a low degree of spatial separation and vice versa?
3) Does the degree of separation vary seasonally?
4) Is the pattern of ecological separation among species of predators different from that among herbivores?

Competition between coexisting species may be reduced through food specialization as well as through temporal and spatial separation. The family Chironomidae includes both predators (belonging primarily to the subfamily Tanypodinae) and microphagous deposit feeders ingesting small particles of living and dead plant and animal matter. However, I feel that within each of these two groups food specialization is not as important a mechanism of resource partitioning as temporal and spatial separation. Most chironomid species appear to be opportunistic in their feeding habits. Sorokin (1966) found that Cricotopus sylvestris assimilated green algae, blue-green algae, diatoms, bacteria and dead Cladocera about equally well, with the assimilation efficiencies ranging from 14-31% for the different food materials. Konstantinov (1958) found that the natural diet of Einfeldia dorsalis larvae included bacteria, diatoms, green algae, higher aquatic plants, protozoans, rotifers and microcrustaceans. In addition, he was able to rear this species on various dried plant matter, yeast extracts and prepared fish food. Hamilton (1965) and Davies (1975) found that the composition of the gut contents of deposit feeders closely resembled that of the sediment taken from the same location as the larvae.

Cummins (1973) gave two reasons why food specialization (monophagy) would not be as advantageous to stream animals as a generalized diet (polyphagy). The abundance of algae and terrestrial leaf litter, important food sources for aquatic animals, fluctuates seasonally. Polyphagy would minimize the effect of such fluctuations. Secondly, the caloric content, and to a lesser degree, the protein composition of food materials available in freshwater environments are quite similar. For monophagy to be successful "the energy (or protein) differences between foods must be greater than the energy required by the selective process" (Cummins 1973).

Hairston et al. (1960) have pointed out that herbivores generally do not deplete their food supply to a level where interspecific competition for food would be important. Coffman et al. (1971) estimated that in Linesville Creek, Pennsylvania, the herbivores utilized only 2-10% of the food available to them.

Brown (1961), Darnell (1961), Mundie (1968), Coffman et al. (1971) and Cummins (1973) found that the food of aquatic animals changes with the age or size of the animal. There is usually a greater similarity between the food eaten by the same size class of different species than between different size classes of the same species. Such ontogenetic changes in feeding may simply be caused by bigger animals being able to ingest bigger particles, or it might be caused by changes in behavior, such as movement to different microhabitats (Hayden and Clifford 1974). Changes in diet may also result from seasonal changes in the availability of foods as observed by Chapman and Demory (1963) and Armitage (1968). The type of food eaten therefore seems to be a function of the developmental stage, which in turn is a function of time. Because of this autocorrelation between food and time, it would be expected that temporally-separated species will also differ in their food.

For the above reasons I decided to concentrate on spatial and temporal separation of the various species and exclude any study of their feeding behavior. Most of 1971 and 1972 were spent on identification of species, association of various life stages and design and testing of sampling equipment. Field work during these two summers was hampered by frequent floods. Most of the data on phenology and microhabitat distribution were collected in 1973 during which there were no floods and by which time I was completely familiar with the identity of the various species and the performance of the various sampling equipment.

II DESCRIPTION OF THE STUDY AREA

A. General Description

The Bigoray River is located 120 km west of Edmonton, Alberta, in the most southern area of muskeg in the province (Fig. 1). The watershed covers 450 km^2, 25% being bogs and fens. The river can be divided into three longitudinal zones (Fig. 2):

1) A headwater zone extends for the first 20-25 km. The average gradient is 0.8%, but in some sections the gradient is as much as 2.0%. Water flows rapidly and the river channel is composed of alternating riffles and pools. The substrate is composed of rocks. Riparian vegetation consists of White Spruce (Picea glauca), Balsam Poplar (Populus balsamifera), Trembling Aspen (Populus tremuloides), Water Birch (Betula occidentalis), Mountain Alder (Alnus tenuifolia) as well as several species of willows (Salix spp.).

2) A middle zone extends for about 50 km. The average gradient is 0.1%. Current velocity may reach 30 cm/sec in constricted areas, below beaver dams and during spates, but normally is less than 1 cm/sec. The stream meanders through sedge fens and bogs covered with Black Spruce (Picea mariana), Tamarack (Larix laricina) and willows. The stream is U-shaped in cross-section, with steep, often undercut, banks. The stream bottom consists of sand, silt and clay; rocks are rare. Aquatic macrophytes are abundant, with Potamogeton richardsonii, Sparganium angustifolium and Hip-

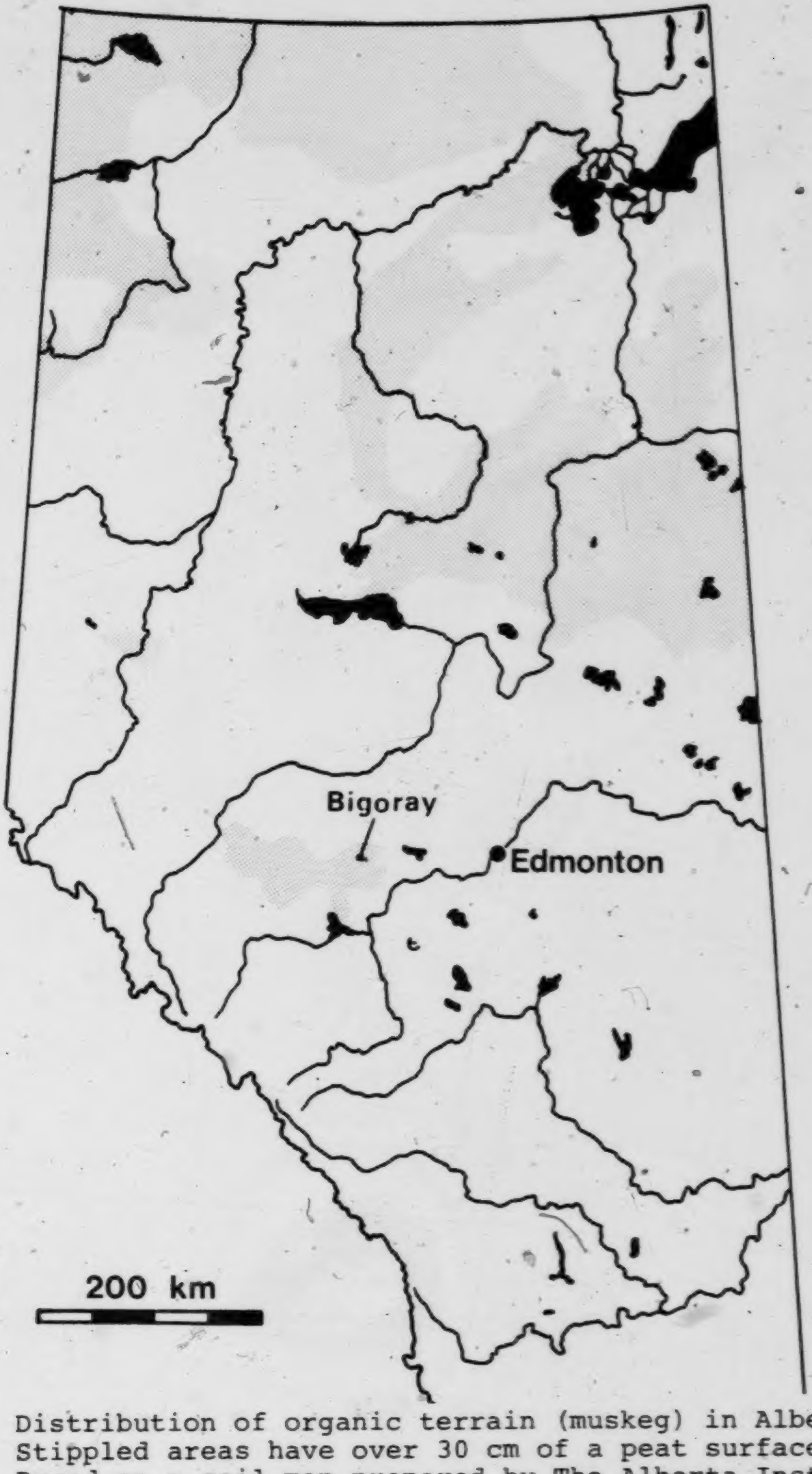

Bigoray
Edmonton
200 km

Fig. 1 Distribution of organic terrain (muskeg) in Alberta. Stippled areas have over 30 cm of a peat surface. Based on a soil map prepared by The Alberta Institute of Pedology.

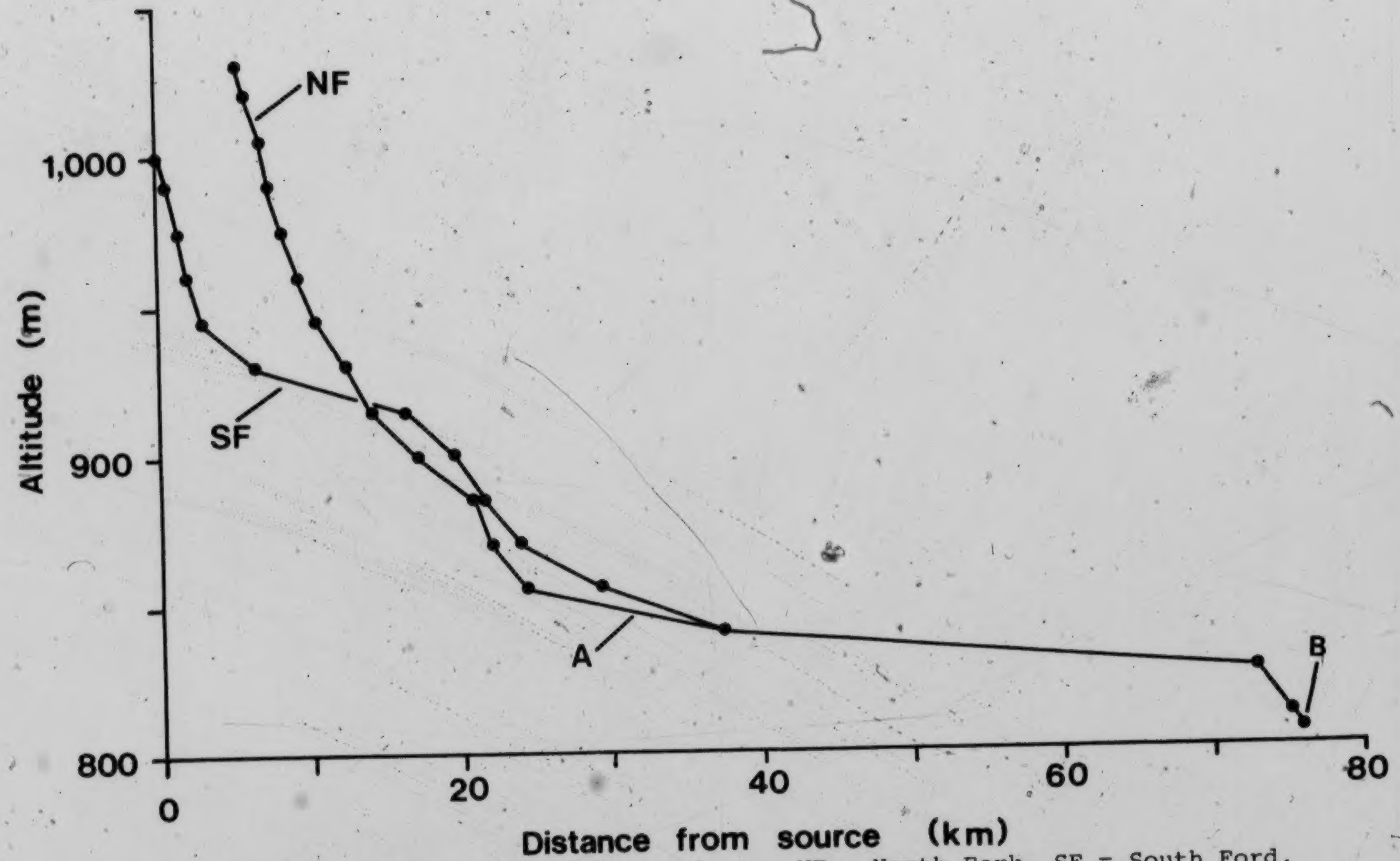


Fig. 2 Longitudinal profile of the Bigoray River. NF = North Fork, SF = South Ford, A = study area, B = confluence with Pembina River.

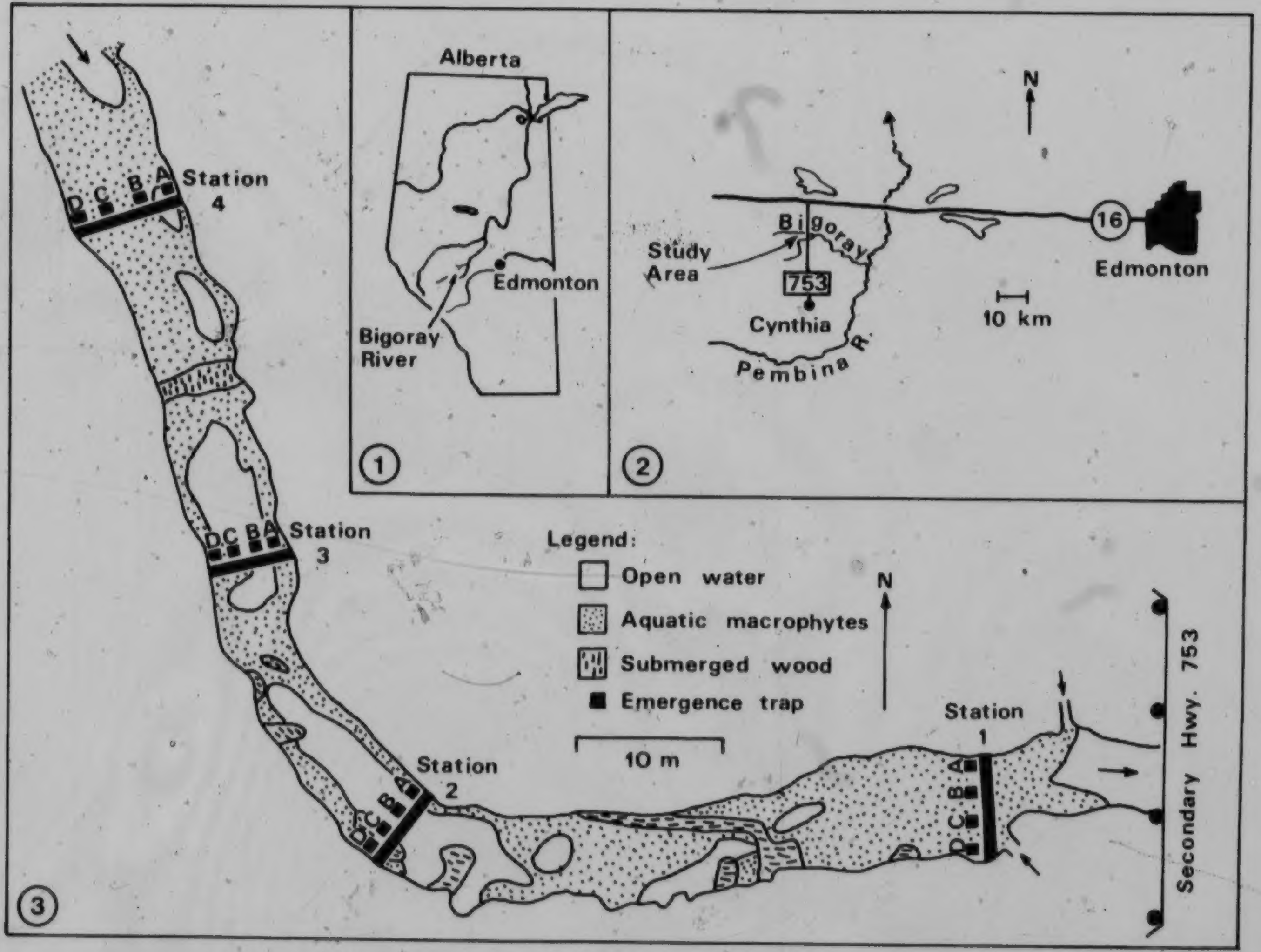
puris vulgaris being the most common. Less abundant are Myriophyllum verticellatum, Callitriche palustris, Ranunculus gmelinii, Polygonium amphibium and the aquatic moss Drepanocladius revolvens. Beaver dams are numerous in this zone.

3) A lower zone, about 5 km long, features a deep gorge cut down to the level of the Pembina River. As in the head-water zone, this area is characterized by a rocky bottom and alternating riffles and pools.

An all-weather gravel road (secondary Highway 753) crosses both forks of the Bigoray River about 4 km above their confluence (Fig.3). A 150-m section of the North Fork, representative of the middle zone and located just upstream from the bridge, was chosen as a study area. Here the stream is of third order and averages about 7 m in width. Guide posts were placed at 5-m intervals along both banks of the study area in order to facilitate mapping of the area and for locating randomly-chosen sampling points (Figs. 4 and 5). These figures also show the cross-sectional outline of the stream at 5-m intervals, as well as the distribution of the major aquatic macrophytes and submerged wood.

B. Description of Aquatic Microhabitats

The amount of aquatic vegetation and submerged wood present in the study area was measured on July 5, August 3 and August 23, 1973. In each 5-m section of the study area a quadrat measuring 0.1 m^2 was chosen at random and all sub-


Alberta
Edmonton
Bigoray River
①
N
Bigoray
Study Area
753
Cynthia
Pembina R.
16
Edmonton
10 km
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Station 4
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Station 3
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Station 1
D C B A
Legend:
Open water
Aquatic macrophytes
Submerged wood
Emergence trap
N
10 m
Secondary Hwy. 753
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Fig. 3 Location of Bigoray River (1,2), and outline map of study area (3).

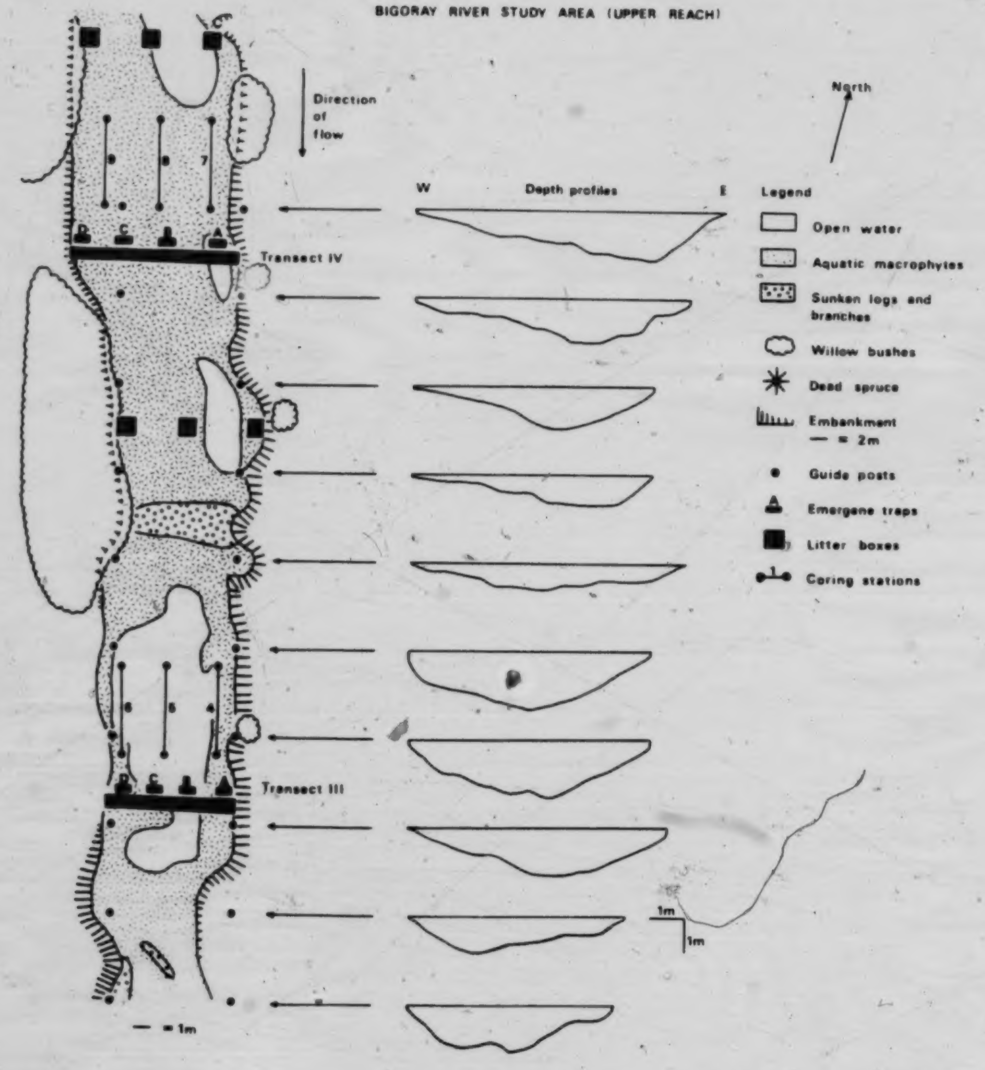

BIGORAY RIVER STUDY AREA (UPPER REACH)
Direction of flow
North
W
Depth profiles
E
Legend
Open water
Aquatic macrophytes
Sunken logs and branches
Willow bushes
Dead spruce
Embankment
— = 2m
Guide posts
Emergence traps
Litter boxes
Coring stations
9
8
7
D
C
B
A
Transect IV
6
5
4
Transect III
1m
1m
— = 1m

Fig. 4 Map of upper reach of Bigoray River study area together with depth profiles.

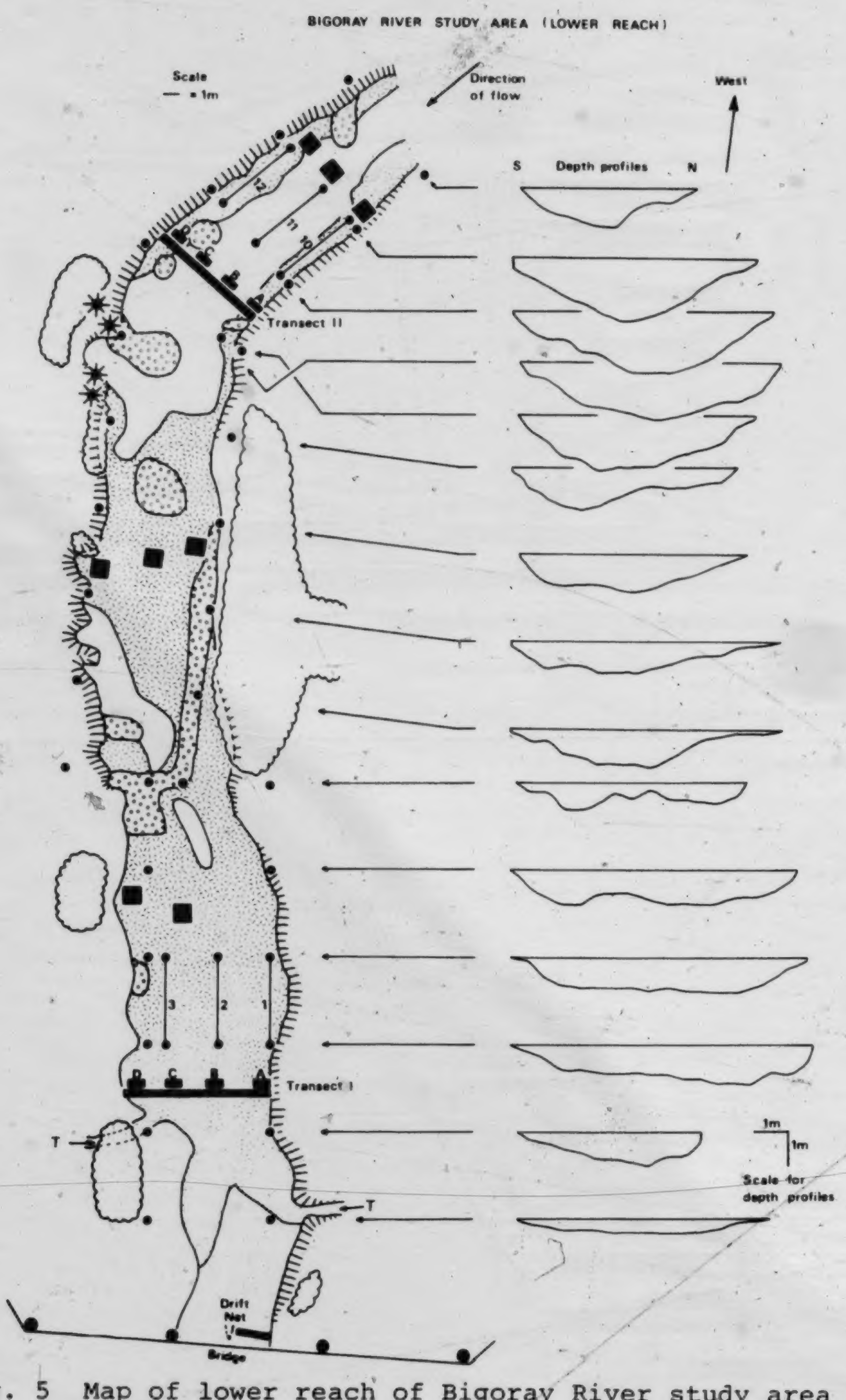

BIGORAY RIVER STUDY AREA (LOWER REACH)
Scale
— = 1m
Direction of flow
West
S
Depth profiles
N
Transect II
3
2
1
D
C
B
A
Transect I
T
T
1m
1m
Scale for depth profiles
Drift Net
Bridge

Fig. 5 Map of lower reach of Bigoray River study area together with depth profiles. T indicates tributary. Other symbols as in Fig. 4.

merged wood and aquatic macrophytes were removed from the quadrats with the aid of SCUBA. The amount of leaf litter and other material falling into the stream during the autumn was measured with floating litter boxes measuring 1 m by 1 m by 25 cm. The litter boxes were positioned in three transects of three boxes each and one transect of two boxes using a stratified random design (Figs. 4 and 5). The litter boxes were checked every 3-7 days between August 30 and October 30, 1973. The surface area of all wood collected from the quadrats was determined. Leaf litter collected from the litter boxes and aquatic macrophytes collected from the quadrats were first separated into taxonomic groups and then dried at 70°C for 24 hours to obtain dry weights.

The upper 2 cm of the bottom sediment were sampled with a plastic corer using a stratified random design. Altogether 73 sediment samples, collected on July 5, September 7 and October 13, 1973, were analyzed for particle size and organic content. The sediment was first washed through four screens with aperture sizes of 1,000, 340, 160 and 80 microns. Sediment fractions were then dried at 70°C for 24 hours and weighed to obtain the dry weight. The five fractions were then combined and ashed in a muffle furnace at 600°C and then reweighed to determine loss on ignition.

The above procedures yielded a quantitative description of the various aquatic microhabitats that occurred in the study area:

1) Submerged wood. The stream banks are composed of peat underlain by glacial till and are therefore easily eroded, especially during periods of high water. Erosion results in a large number of trees and bushes falling into the stream. During the 3 years of field work, 10% of the stream bank was changed as a result of erosion or deposition; also one 10-m high spruce tree collapsed across the stream. Beavers also deposit a considerable amount of wood in the stream. Hence, there is a large amount of wood in the river. Based on the 67 quadrat samples, the surface area of the submerged wood ranged from 0.0-5.1 m^2 per square meter of stream, with the mean value being 0.6 m^2 (Tables I, II and III).

2) Aquatic macrophytes. These first appeared in early June and continued to grow until the end of August. Based on the 67 quadrat samples the mean weight of aquatic macrophytes was 115 gm/m^2 at the height of the growing season (August 29, 1973), with the highest recorded value being 442 gm/m^2. Sparganium and Potamogeton accounted for 65% and 25%, respectively, of the total aquatic macrophytes on a dry weight basis (Tables I, II and III).

3) Filamentous algae. This was present in small amounts during June and July, but increased to 10 gm dry weight/m^2 during August (Tables I, II and III). At that time it formed extensive mats in many parts of the study area.

4) Sponges. Colonies of Spongilla were found growing on submerged wood at depths below 0.5 m. A single colony

TABLE I The surface area (m^2) of submerged wood and the dry weight (gm) of aquatic macrophytes and filamentous algae in the Bigoray River on July 5, 1973. Each quadrat covered 0.1 m^2. Total weight includes only the macrophytes and algae.

Quadrat	Subm. Wood	Sparganium	Potamogeton	Hippuris	Callitriche	Fila. Algae	Total Weight
1	0.00	20.99	0.00	0.00	0.00	0.16	20.99
2	0.51	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	12.34	0.00	0.00	0.00	0.05	12.34
4	0.00	8.00	0.00	0.00	0.00	0.00	8.00
5	0.01	3.10	0.00	0.00	0.00	0.00	3.10
6	0.02	1.21	1.22	3.71	0.00	0.00	6.14
7	0.00	1.66	5.66	0.00	0.00	0.00	7.32
8	0.02	0.14	7.20	0.00	0.00	0.00	7.34
9	0.02	0.21	0.00	0.00	0.00	0.00	0.21
10	0.03	3.07	0.00	0.00	0.00	0.00	3.07
11	0.21	0.00	2.36	0.00	0.00	0.00	2.36
12	0.00	0.00	0.00	0.00	0.03	0.00	0.03
13	0.01	4.30	0.00	0.00	0.00	0.00	4.30
14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16	0.03	0.73	1.91	0.00	0.00	0.00	2.64
17	0.03	0.00	0.00	0.00	0.00	0.00	0.00
18	0.00	0.32	0.00	0.00	0.00	0.00	0.32
19	0.02	0.00	2.03	0.00	0.00	0.00	2.03
20	0.00	4.15	0.00	0.00	0.00	0.00	4.15
21	0.13	0.17	11.11	0.00	0.00	0.00	11.28
22	0.13	0.00	0.00	0.00	0.00	0.00	0.00
23	0.11	10.44	0.00	2.36	0.00	0.02	12.80
Total	1.28	70.83	31.49	6.07	0.03	0.23	108.42
Mean	0.06	3.08	1.37	0.26	0.00	0.01	4.71

TABLE II The surface area (m^2) of submerged wood and the dry weight (gm) of aquatic macrophytes and filamentous algae in the Bigoray River on August 3, 1973. Each quadrat covered 0.1 m^2. Total weight includes only the macrophytes and algae.

Quadrat	Subm. Wood	Sparganium	Potamogeton	Hippuris	Callitriche	Fila. Algae	Total Weight
1	0.00	0.14	0.00	0.00	0.00	0.00	0.14
2	0.26	1.49	18.62	0.00	0.00	0.00	20.11
3	0.02	0.00	0.00	0.00	0.00	0.00	0.00
4	0.03	11.15	0.00	0.00	0.00	0.00	11.15
5	0.28	5.63	0.00	0.00	0.00	0.00	5.63
6	0.13	22.77	3.30	0.00	0.00	0.00	26.07
7	0.00	35.75	0.00	0.00	0.00	0.00	35.75
8	0.06	3.12	1.48	0.23	0.00	0.00	4.83
9	0.00	0.14	0.34	0.00	0.01	0.84	1.33
10	0.01	28.81	0.00	0.00	0.00	0.00	28.81
11	0.01	0.00	0.97	0.00	2.65	0.00	3.62
12	0.00	4.30	0.00	0.00	0.00	0.00	4.30
13	0.28	0.00	0.00	0.00	0.00	0.00	0.00
14	0.17	0.00	0.00	0.00	0.00	0.00	0.00
15	0.05	34.77	13.36	0.00	0.00	0.00	48.13
16	0.07	12.53	0.00	0.00	0.00	0.00	12.53
17	0.10	0.00	0.00	0.00	0.00	0.00	0.00
18	0.01	0.75	1.61	4.49	0.00	0.00	6.85
19	0.11	0.25	0.00	0.00	0.00	0.00	0.25
20	0.00	0.00	9.74	0.00	0.41	0.00	10.15
21	0.01	1.48	0.00	0.00	0.00	0.00	1.48
22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total	1.60	163.08	49.42	4.72	3.07	0.84	221.13
Mean	0.07	7.41	2.25	0.21	0.14	0.04	10.05

TABLE III The surface area (m^2) of submerged wood and the dry weight (gm) of aquatic macrophytes and filamentous algae in the Bigoray River on August 29, 1973. Each quadrat covered 0.1 m^2. Total weight includes only the macrophytes and algae.

Quadrat	Subm. Wood	Sparganium	Poramogeton	Hippuris	Callitriche	Fila. Algae	Total Weight
1	0.06	6.32	0.29	0.00	0.00	0.00	6.61
2	0.09	8.60	8.24	0.00	0.00	0.00	16.84
3	0.21	5.10	4.40	4.24	0.00	0.86	14.60
4	0.15	3.55	9.62	0.00	0.00	0.62	13.79
5	0.19	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	31.01	0.00	0.00	0.00	0.00	31.01
7	0.00	22.68	0.00	0.00	0.00	0.00	22.68
8	0.10	44.20	0.00	0.00	0.00	0.00	44.20
9	0.00	0.00	9.80	0.00	0.00	9.30	19.10
10	0.00	10.94	0.00	0.00	0.00	4.51	15.45
11	0.00	0.00	15.45	0.00	0.00	3.38	18.83
12	0.00	1.87	1.01	1.68	0.00	0.83	5.39
13	0.09	1.39	0.00	0.00	0.04	0.10	1.53
14	0.10	0.00	0.00	0.00	0.00	0.00	0.00
15	0.04	0.43	3.49	0.00	0.01	0.32	4.25
16	0.03	3.85	0.00	0.00	0.00	0.00	3.85
17	0.01	1.13	5.29	0.00	0.00	0.71	7.13
18	0.03	0.00	0.00	0.00	0.00	0.00	0.00
19	0.00	2.14	0.00	0.00	0.00	1.78	3.92
20	0.00	0.14	6.88	0.00	0.15	0.00	7.17
21	0.02	4.42	1.37	0.00	0.00	0.00	5.79
22	0.00	7.61	2.29	0.00	0.00	0.00	9.90
Total	1.12	155.38	68.13	5.92	0.20	22.41	252.04
Mean	0.05	7.06	3.10	0.27	0.01	1.02	11.46

was collected in one of the 63 quadrat samples. Assuming that the colonies increased in size but not in numbers between the three bottom surveys, then the density of colonies was about one for every 6 m^2 of stream.

5) Rocks. A few pebbles were found during the three bottom surveys. The average surface area of these was 3 cm^2 per square meter of stream.

6) Leaf litter. An average of 13.3 gm dry weight of allochthonous material, mainly willow leaves, fell on each square meter of stream between August 30 and October 30, 1973 (Table IV). Litter fall was concentrated underneath overhanging bushes and reached a maximum of 152.6 gm/m^2 in such locations.

7) Bottom sediment. Dry weight of the five size classes of sediment was expressed as a percentage of the dry weight of the whole sample. The percentages were then cumulated starting with the coarsest fraction and working towards the finest. The cumulative percentages were then plotted against particle size expressed in phi (ø) units (phi is the negative logarithm to the base two of the particle size in millimeters). A conversion table (Page 1955) can be used to facilitate the conversion between phi and millimeter units. When plotted on probability paper, such cumulative size-frequency plots form nearly straight lines (Fig. 6), allowing the mean particle size of the sediment to be read directly from the graph (i.e., the mean size is at the point where

TABLE IV Input of terrestrial litter to the Bigoray River during September and October, 1973. Units are in grams of dry weight.

	Rate of litter fall gm/m^2/day	Cumulative litter fall gm/m^2
August 30-September 3	0.1	0.4
September 3-September 6	0.5	1.9
September 6-September 11	1.0	6.9
September 11-September 14	0.9	9.6
September 14-September 17	0.1	9.9
September 17-September 24	0.1	10.6
September 24-October 2	0.2	12.2
October 2-October 9	0.1	12.9
October 9-October 30	0.02	13.3

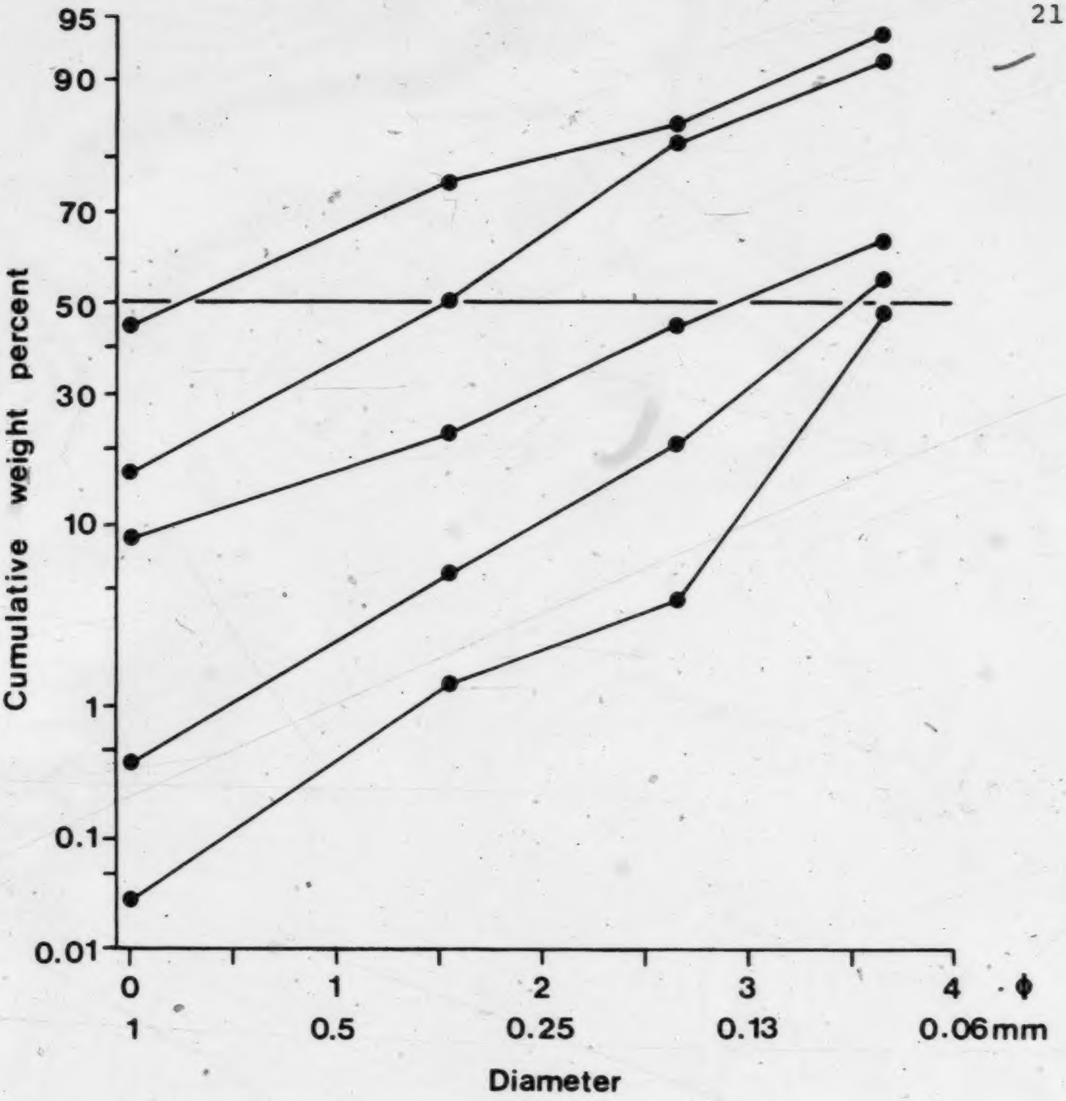


Fig. 6 Cumulative frequency curves for particle sizes in upper 2 cm of Bigoray River sediment. Five curves indicate range of values encountered. Probability scale used for ordinate.

the cumulative plot intersects the 50% mark). The mean grain size of the upper 2 cm of the sediment was found to be 2.4 ø (0.19 mm) and ranged from 0.3 ø (0.98 mm) to 4.1 ø (0.06 mm) (Fig. 7). According to the Wentworth scale, the composition of the sediment ranged from very fine sand to coarse sand with the average being fine sand.

The difference in weight between sediment dried at 70°C and 500°C can be taken as a good approximation of the organic content of the sediment (Davies 1975). When measured in this manner, the percentage of organic matter in the upper 2 cm of the sediment varied from 1-60% with a mean of 6% (Fig. 8).

The sediment consisted of 1-3 vertical strata (Fig. 9). The lowermost layer consisted of hard clay which was almost dry to the touch and which generally stuck to the inside of coring tubes. The clay either lay exposed to the water above it, or else was covered with up to 5 cm of sand, or with up to 5 cm of detritus, or with a layer of sand which in turn was covered by a layer of detritus. The 3-layer stratification was the most common.

C. Comparison of the Decomposition Rates of Sparganium and Willow Leaves

Small wire cages with a mesh size of 1 cm were filled with 15 gm of either fresh *Sparganium* or willow leaves. Pairs of cages, one filled with *Sparganium* and the other

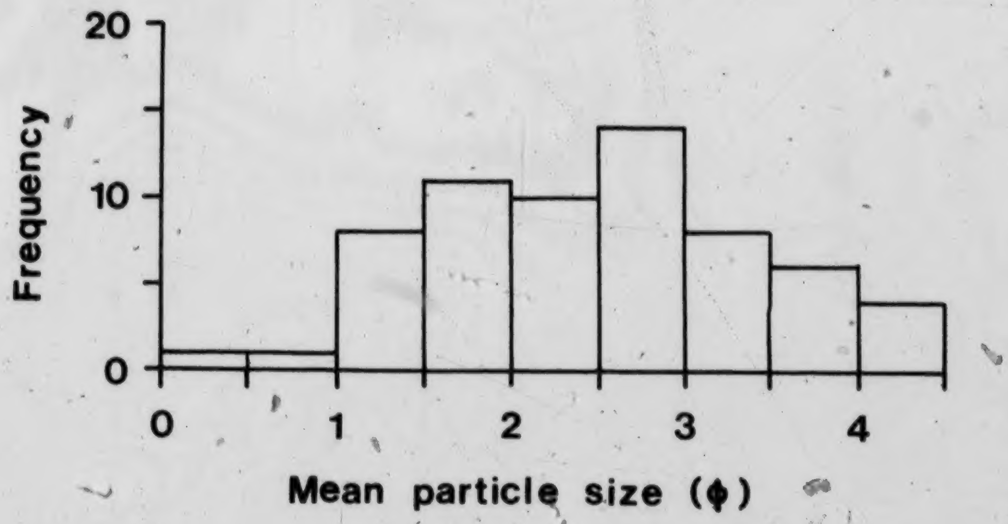


Fig. 7 Variation in mean particle size in 73 samples from upper 2 cm of Bigoray River sediment.

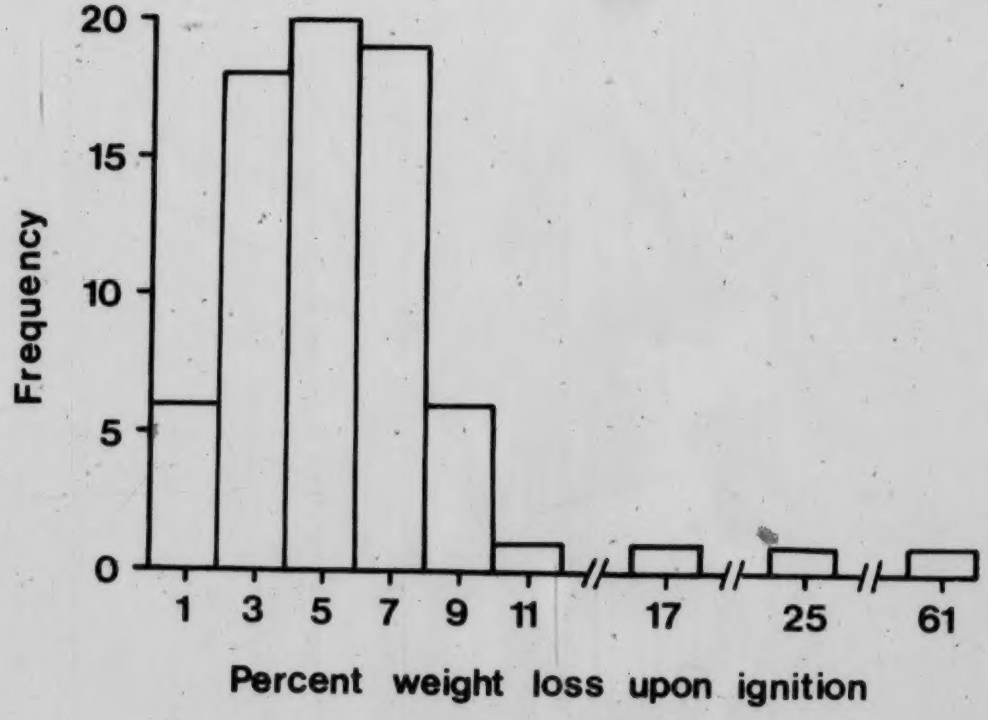


Fig. 8 Variation in percentage of organic matter in 73 samples from upper 2 cm of Bigoray River sediment.

Fig. 9 Vertical stratification of sediment in the Bigoray River. Photograph shows a 5-cm deep layer of black detritus covering a 5-cm deep layer of brown sand, which in turn covers the grey clay layer.

with willow leaves, were suspended 25 cm above the bottom of the stream at Transects I, II and IV on September 24, 1973 (Figs. 3 and 4). After 2, 4, 6 and 12 weeks (October 9, October 24, November 7 and December 21) of immersion, one pair of cages was removed from each transect (i.e., altogether 3 cages filled with Sparganium and 3 cages filled with willow leaves). All animals were removed and the contents of the cages dried at 70°C. The experiment was terminated on December 21 because of difficulty in keeping the cages from being frozen into the ice. After the 12 weeks of immersion, Sparganium had lost 79% of the original dry weight, whereas willow leaves had lost only 50% (Table V).

D. Seasonal Changes in the Major Plant Components of the Bigoray River

Quantitative information on the standing stocks of aquatic macrophytes, input of terrestrial leaves to the stream, and decomposition rates of Sparganium and willow leaves can now be combined with qualitative field observations to obtain a picture of the seasonal changes in the major plant components of the Bigoray River (Fig. 10). Since the amount of submerged wood does not undergo noticeable seasonal changes, it has been omitted from Figure 10. However, the amount of wood may be altered occasionally through floods and windstorms. Also, beavers bring more wood into the stream during the autumn than at other times of the year,

TABLE V Percentage weight loss of willow leaves and *Sparganium* after being immersed in the Bigoray River for various periods of time.

Plant Type		Oct. 9 2 wks.	Oct. 24 4 wks.	Nov. 7 6 wks.	Dec. 21 12 wks.
		Date and length of time immersed			
Leaves					
Replicate 1		15	23	23	49
Replicate 2		21	25	24	54
Replicate 3		18	23	22	48
	Mean	18	24	22	50
Sparganium					
Replicate 1		0	31	57	77
Replicate 2		14	24	40	81
Replicate 3		5	29	48	81
	Mean	6	28	48	79

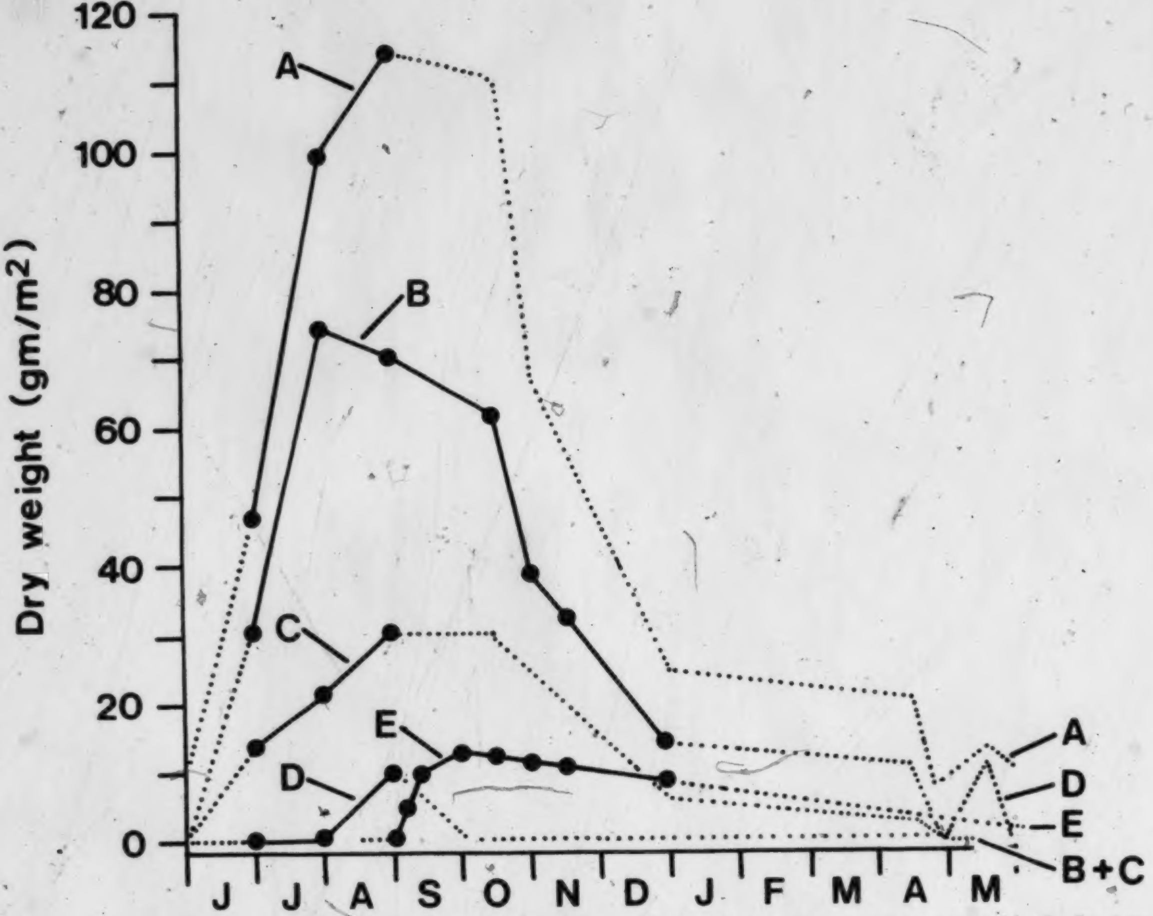


Fig. 10 Seasonal changes in biomass of aquatic vegetation and autumn-shed leaves in the Bigoray River. A = total aquatic macrophytes, B = *Sparganium*, C = *Potamogeton*. D = filamentous algae, E = autumn-shed leaves. Solid lines based on quantitative data, dotted lines based on qualitative field observations.

and this may result in seasonal increases in wood near lodges and dams. However, there were no lodges or dams in the study area.

Sparganium and Potamogeton shoots began to appear in early June. The maximum standing stock of Sparganium occurred at the end of July, whereas Potamogeton reached its peak biomass at the end of August. The plants decomposed rapidly after the middle of October, and they had decreased to about 20% of the maximum standing stock by the end of December. The rate of decomposition quite likely decreased after December, since field observations indicated that a substantial amount of the Sparganium and Potamogeton had been frozen into the ice, which usually reached a thickness of 50 cm by this time. Following the breakup of ice during the second half of April, the breakdown of the remaining plant material was quickly completed through attrition by ice floes and increased microbial decomposition resulting from the spring rise in water temperature. Neither old aquatic macrophytes nor new growth was observed during May of the three years of field work.

The filamentous algae were abundant during August and September, and field observations indicated a similar peak during May. These algal peaks may have been partly due to the release of dissolved organic matter from the breakdown of the aquatic macrophytes (Novak et al. 1975).

Input of terrestrial leaf litter to the stream occurs primarily during September. Since the leaves sink very quickly to the bottom of the stream, their decomposition rate is not influenced by the ice, and they decompose at a constant rate during the autumn and winter. Some remains of last year's leaves were seen during the bottom survey carried out July 5, 1973 but not on the two subsequent surveys.

In the Bigoray River the amount of allochthonous organic matter is at least an order of magnitude less than the amount of autochthonous organic matter. This condition, which appears to be generally characteristic of northern brown-water streams, is the converse of the condition found in woodland and mountain streams (Hynes 1970). The generalization that allochthonous organic matter is the major source of energy in lotic systems should therefore be used with care.

E. Seasonal Changes in Surface Area Available for Colonization by Aquatic Invertebrates

Bottom sediment, submerged wood and aquatic macrophytes all provide surface areas that can be colonized by aquatic invertebrates. Therefore, the substrate area available for colonization underneath a 1-m^2 area of stream surface is usually considerably greater than 1 m^2. This can be calculated by converting the dry weights of macrophytes given in Tables I, II and III to their equivalent surface areas using the conversion factors given in Table VI. The table

TABLE VI The relationship between surface area, fresh plant volume and dry weight of aquatic plants in the Bigoray River. Numbers in brackets give the sample size. Other numbers are means ± 2 standard errors.

Plant Type		Area/Weight (cm^2/gm)	Volume/Weight (cm^3/gm)	Area/Volume (cm^2/cm^3)
Sparganium	(8)	707 ± 13	19.7 ± 1.2	37.6 ± 2.4
Potamogeton	(10)	1,028 ± 116	14.0 ± 0.9	73.6 ± 7.2
Moss	(10)	1,526 ± 136	15.2 ± 1.5	103 ± 9.4
Hippuris	(9)	2,549 ± 638	20.9 ± 2.2	122 ± 9.6
Fil. algae	(5)	-	23.5 ± 5.6	-
Willow leaves	(9)	250 ± 9	-	-

also gives the relationships between plant volume and weight and between plant area and volume.

The surface area of the macrophytes is then added to the surface area of the bottom sediment and submerged wood, these two remaining relatively constant at 1.0 m^2 and 0.6 m^2 per square meter of stream, respectively. Such calculations show that the substrate area available for colonization is at a minimum of 1.6 m^2 per square meter of stream surface in late winter and early spring, when there are no macrophytes. The substrate area then increases to 10.4 m^2 per square meter of stream in late August, when the macrophytes reach their maximum biomass. The effective area available for colonization by aquatic invertebrates therefore varies almost tenfold over the course of a year.

F. Physical and Chemical Parameters of the Bigoray River

Seasonal changes in water temperature and water level are shown in Figure 21. Seasonal changes in other physical and chemical parameters have been summarized by Clifford (1978), and will only be briefly outlined below. Stream discharge is seldom over 1 m^3/sec and decreases to as little as 0.06 m^3/sec during winter. Dissolved oxygen is always high, never falling below 50% saturation. Because of the large amount of aquatic plants, there are probably considerable diel fluctuations in dissolved oxygen during the summer, but measurements have not been made. The pH is always above

7.0 and rarely exceeds 8.3. Water color is brown (200 ppm platinum) during the ice-free period because of the inflow of humic and fluvic acids from the surrounding muskeg and the decomposition of aquatic vegetation (Fig. 11). Color decreases gradually during winter and reaches a minimum of approximately 50 ppm before the start of the spring thaw. The specific conductance reaches a maximum of 550 µmohs during the spring breakup. Conductivity remains low until July and then gradually increases to the winter maximum. Concentration of dissolved solids varies between 50 and 450 ppm, and total hardness and total alkalinity vary between 50 and 300 ppm $CaCo_3$, with a seasonal pattern of variation similar to conductivity. Calcium hardness varies between 50 and 170 ppm $CaCO_3$. Silica varies between 3 and 8 ppm. Nitrate is usually less than 0.10 ppm, ortho-phosphate less than 0.2 ppm, sulfate less than 14 ppm, and iron less than 2 ppm.

Fig. 11 Photograph showing characteristic brown color of the Bigoray River during the ice-free period.

III METHODS

A. Emergence Traps

The emergence trap used in this study consisted of a screen-covered box attached to a float (Figs. 12 and 13). The bottom of the box, covering 0.1 m^2 of stream surface, was open, and the top was covered with a hinged lid. The sides of the box and the lid were covered with nylon chiffon having a mesh size of 0.2-0.3 mm. Inside the box were two upward-projecting flanges (D), which prevented the chironomids from falling back into the water. A sloping roof (I), covered with clear plastic film, was attached to the lid to keep out rain.

The float consisted of two styrofoam blocks (A) separated by two strips of wood (B). The box was attached to the float by means of four angle brackets (F), which fitted onto studs projecting from the styrofoam blocks. The float could slide up or down along two aluminum poles (J), so that the bottom of the box was always positioned exactly at the water surface. The bottom of the box was adjusted level with the water surface by placing washers underneath the angle brackets.

To remove chironomids caught in the trap, a plastic plate (C) was first pushed into grooves underneath the box in order to seal the bottom. The box was then lifted off the float and taken to the shore. The lid, hinged to the back of the box (K) and kept closed by two hooks at the

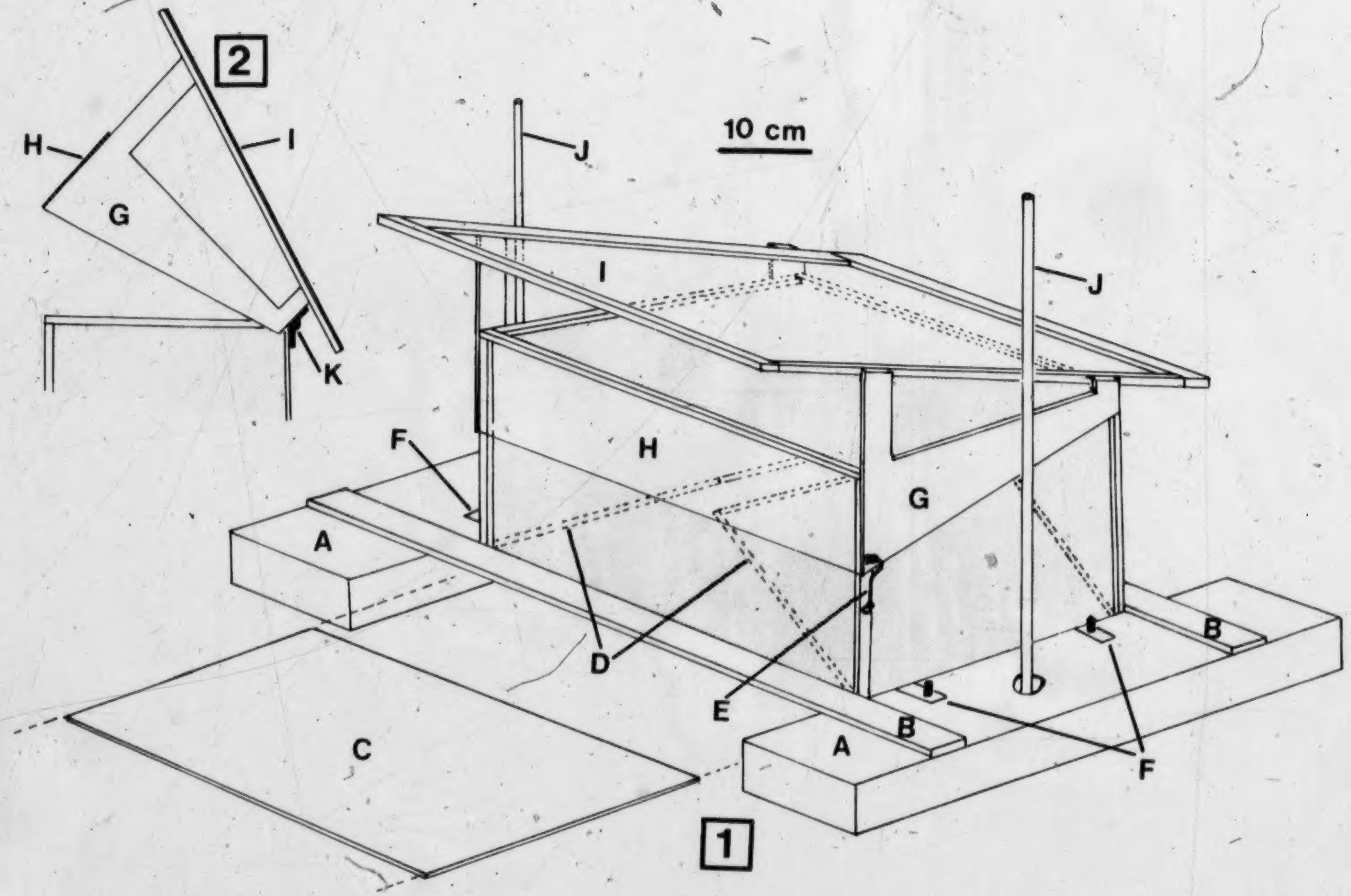

2
H
I
G
K
J
10 cm
J
I
F
H
G
A
D
E
B
A
B
F
C
1

Fig. 12 Emergence trap with lid closed (1) and open (2). Different parts described in text. Scale: 1 cm = 5 cm.

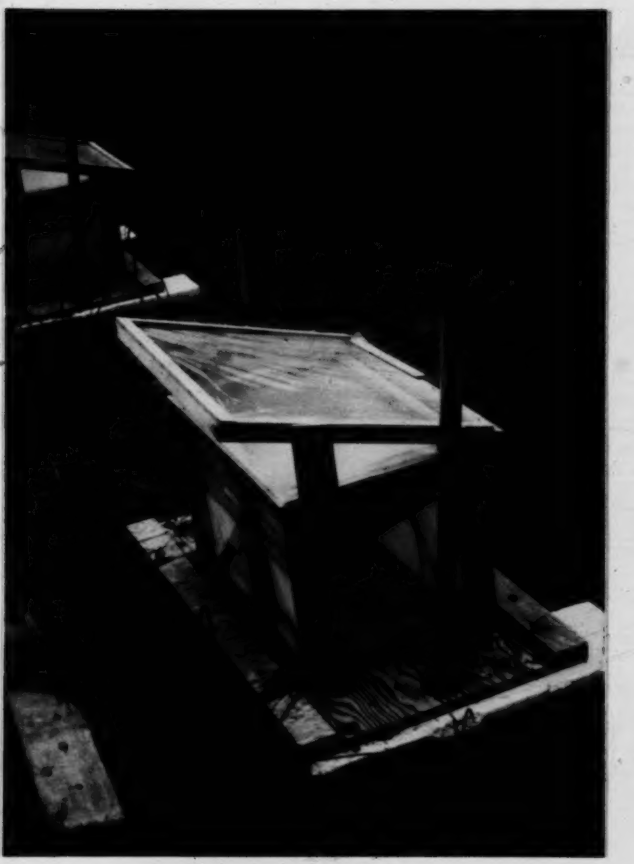


Fig. 13 Closeup of two emergence traps at Transect I. Notice heavy growth of Sparganium and lack of any noticeable current. Downstream is to left of photograph.

front (E), was then carefully lifted a few centimeters until an aspirator could be inserted underneath the plastic skirt (H). The plastic skirt along the front and a wooden skirt along the sides (G) hung down from the lid and kept the chironomids from escaping when the lid was lifted.

Sixteen emergence traps were arranged in four transects of four traps as shown in Figures 4 and 5. The traps were reached by means of long, wooden gangplanks, which could be raised or lowered according to the water level (Fig. 14). When not in use, the gangplanks were lifted out of the water to prevent interference with the emergence traps. During 1973 the traps were in operation for the entire emergence season and were checked at intervals of 2 to 9 days. The dates of the 36 sampling intervals in 1973 were:

1) April 25-30
2) April 30-May 3
3) May 3-8
4) May 8-11
5) May 11-15
6) May 15-18
7) May 18-21
8) May 21-24
9) May 24-29
10) May 29-June 1
11) June 1-4
12) June 4-7
13) June 7-11
14) June 11-14
15) June 14-18
16) June 18-21
17) June 21-25
18) June 25-July 1
19) July 1-6
20) July 6-11
21) July 11-15
22) July 15-21
23) July 21-26
24) July 26-31
25) July 31-Aug.4
26) Aug. 4-10
27) Aug. 10-14
28) Aug. 14-23
29) Aug. 23-25
30) Aug.25-30
31) Aug.30-Sept.3
32) Sept. 3-10
33) Sept. 10-17
34) Sept. 17-24
35) Sept.24-Oct.1
36) Oct. 1-9

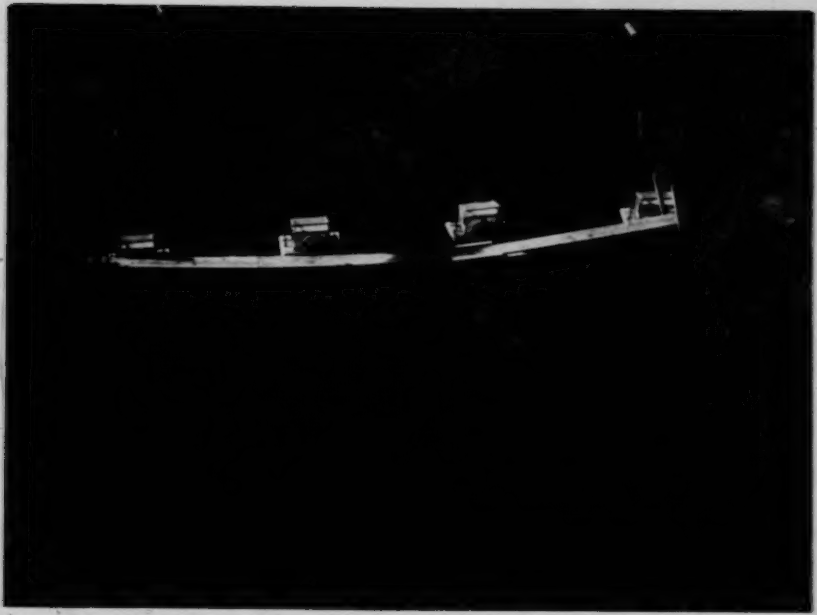


Fig. 14 Photograph of emergence traps at Transect I as viewed from bridge on September 6, 1973.

For traps without the inside flanges, there was a significant (P < 1%) reduction in the number of chironomids caught as the sampling interval increased. Over the same 4-day interval, traps that were sampled once at the end of the 4 days caught only 32% as many chironomids as traps emptied every day during the 4-day interval. For traps with inside flanges, the length of the sampling interval had no significant (P > 5%) effect of the number of chironomids caught.

Completely opaque traps (i.e., covered with black plastic) caught only 33% as many chironomids as the traps covered with netting transmitting 70% of the light (P < 1%). Because most chironomids emerged in the evening, the small shading effect caused by the netting was assumed to have no significant effect on the number of chironomids caught. Fluctuations in current velocity also had no effect on number of chironomids caught (Fig. 15).

B. Bottom Corer

Chironomid larvae living in or on the bottom sediment were collected with a bottom corer (Fig. 16). It consisted of a vertical plexiglass tube (A) 25 cm long and having an inside diameter of 4.4 cm (area = 15.2 cm^2). The top of the tube was attached flush with a horizontal plate (C), which was surrounded by a 2-cm high wall (D). Underneath the free section of the plate was glued a bakelite lid (Q) of one of the collecting jars, and a 4.4-mm diameter hole (R) was

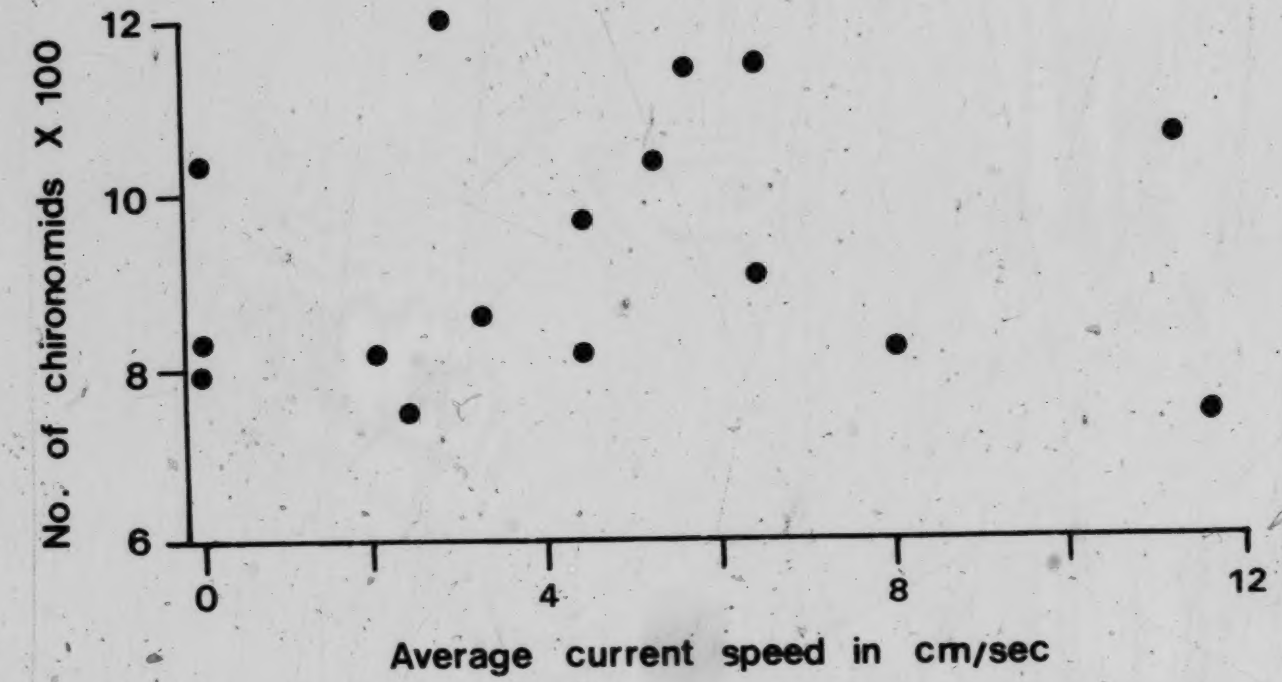
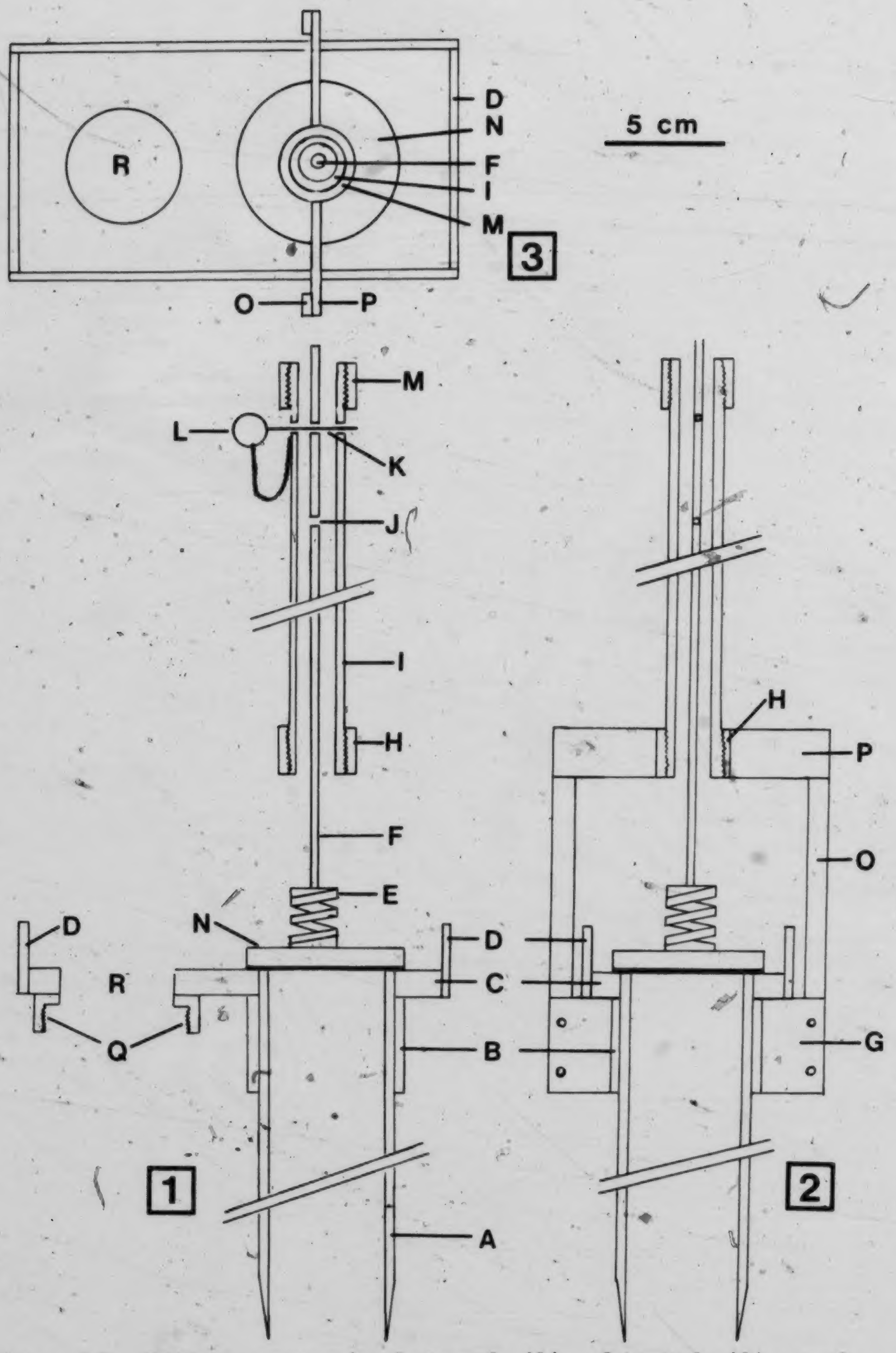


Fig. 15 Relationship between average current speed under an emergence trap and number of chironomids caught in the trap. Data cover the period from May 8 - October 1, 1978.


D
N
F
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3
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5 cm
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Q
D
C
B
A
1
H
P
O
D
C
B
G
2

Fig. 16 Bottom corer in lateral (1), frontal (2), and dorsal (3) view. Different parts described in text.

drilled through both the plate and the lid.

The coring tube was attached to a 1.5-m long aluminum pole (I) by means of a stirrup. The stirrup consisted of a metal collar (B) fitted around the top of the coring tube, two flanges (G) extending laterally from the collar and at right angles to the long axis of plate C, two vertical (O) and two horizontal (P) metal strips, and a coupling (H) that fitted onto the end of the pole. Another coupling (M) provided a suitable knob for pushing the corer into the sediment. The closing mechanism consisted of a metal disc (N) with a layer of soft rubber on the bottom. The metal disc was attached to a compression spring (E) that was attached to an aluminum rod (F) extending along the inside of pipe I.

Prior to collecting a sediment sample, the rod and attached disc were raised and kept in position by pushing pin L through the lowermost hole (J) drilled through the rod. After the corer was pushed into the sediment, pin L was pulled out of hole J and the rod pushed downward until the pin could be inserted into hole K. The compression spring now held the metal disc tightly against the top of the coring tube. The sediment sample was then retrieved as follows:

Step 1. (Fig. 17A). The corer was gently swayed back and forth to free it from the surrounding sediment and prevent the formation of a vacuum underneath the sediment sample (S) when the corer was pulled up.

Step 2. (Fig. 17B). After lifting the corer to the

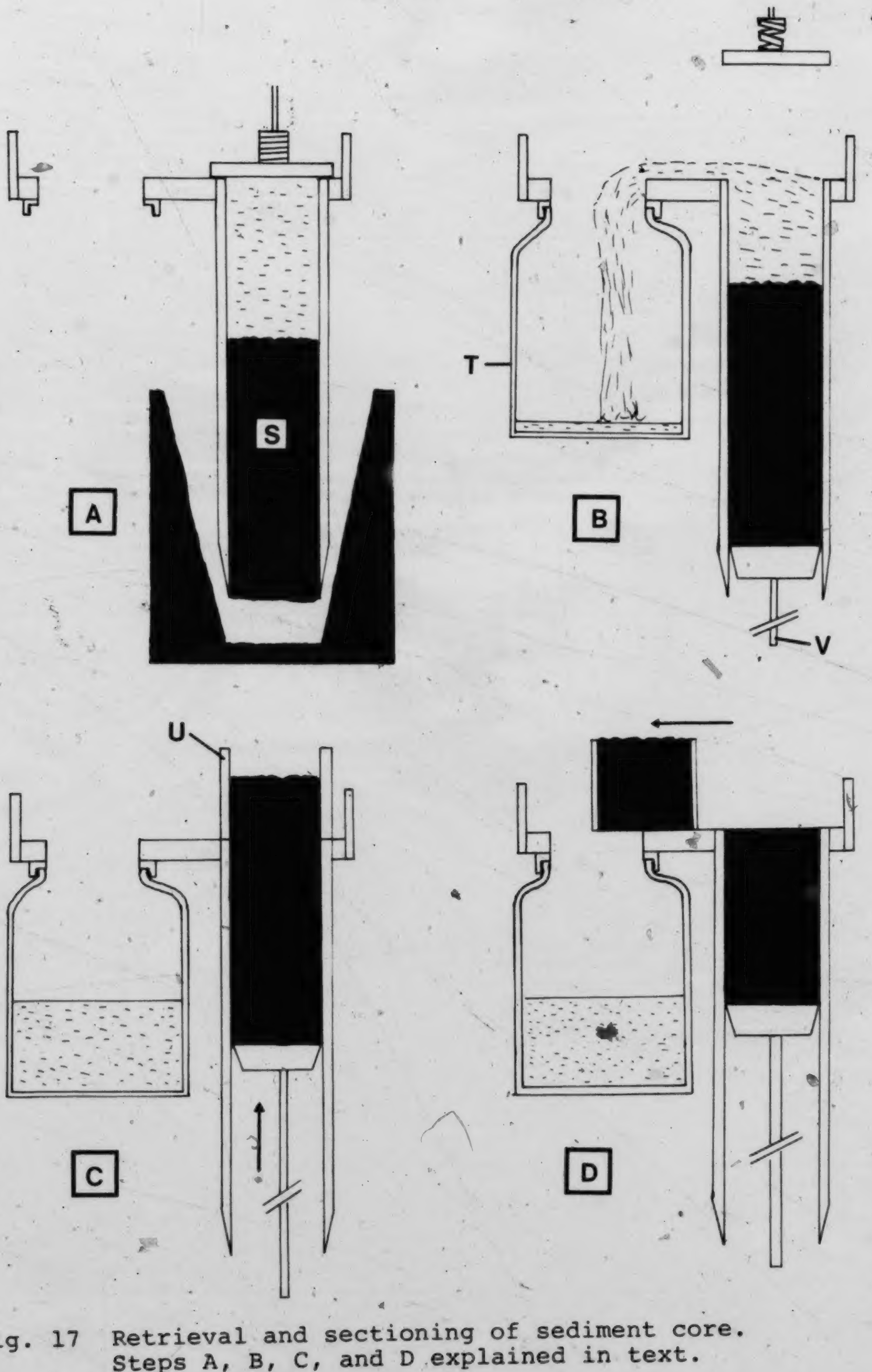

Fig. 17 Retrieval and sectioning of sediment core. Steps A, B, C, and D explained in text.

surface, a plunger (V) was inserted into the bottom of the coring tube, a collecting jar was screwed into the bakelite lid, and disc N was raised. The plunger was then carefully pushed upwards, so that water above the sediment sample flowed across the horizontal plate and into the collecting jar.

Step 3. (Fig. 17C). Once the top of the sediment sample had been pushed flush with the top of the coring tube, a 2-cm high plastic cylinder (U), with an inside diameter of 4.4 cm, was placed above the coring tube and the sediment sample pushed up into the cylinder.

Step 4. (Fig. 17D). Once the top of the sediment sample was flush with the top of the cylinder, it was slid over top of the collecting jar and the sediment sample washed into the jar.

By replacing the full collecting jar with a new one and repeating steps 3 and 4, the sediment core could be divided into a number of sections, each 2 cm long. Sediment samples were collected from 12 stations, with three stations located near the sides and the middle of the stream just upstream from each of the four transects (Figs. 4 and 5). Each station was delimited by two poles spaced 5 m apart lengthwise to the river. On each sampling date, one sample was taken at each station by selecting a point at random between the pair of poles. Sediment samples were collected on the following dates:

1971: Nov. 1; 1972: March 9, May 31, June 20, July 5 and 25, Aug. 8, Sept. 7, Oct. 13 and Nov. 20; 1973: Feb. 12, March 8, May 3 and 30, June 11 and 21, July 11 and 31, Aug. 20, Sept. 10 and Oct. 2. Altogether 252 sediment samples were collected (12 samples x 21 dates).

C. Aquatic Macrophyte Samplers

Chironomid larvae occurring on aquatic vegetation, submerged wood and sponges were collected with two samplers described by McCauley (1975b). Individual shoots of Potamogeton and Hippuris, clumps of moss and filamentous algae, and lengths of submerged wood and attached sponge colonies were collected with Sampler A (Fig. 18). The plexiglass tube (B), with an inside diameter of 10 cm and a length of 80 cm, was pushed over the material to be sampled and then the trigger (H) was pulled. This released spring F, which then pushed blade C across the bottom of the tube, cutting off the material being collected. A net with a mesh size of 80 µ was then attached to the top of the tube (J) and the tube inverted so that the water drained through the net. The blade was able to cut through submerged branches up to 2 cm in diameter.

Larvae living on Sparganium were collected with Sampler B (Fig. 19). The sampler was clamped to the stern of a boat with wing bolts 0_1 and 0_2. Wing bolts M_1 and M_2 were then loosened and the height of the base plate (C) adjusted

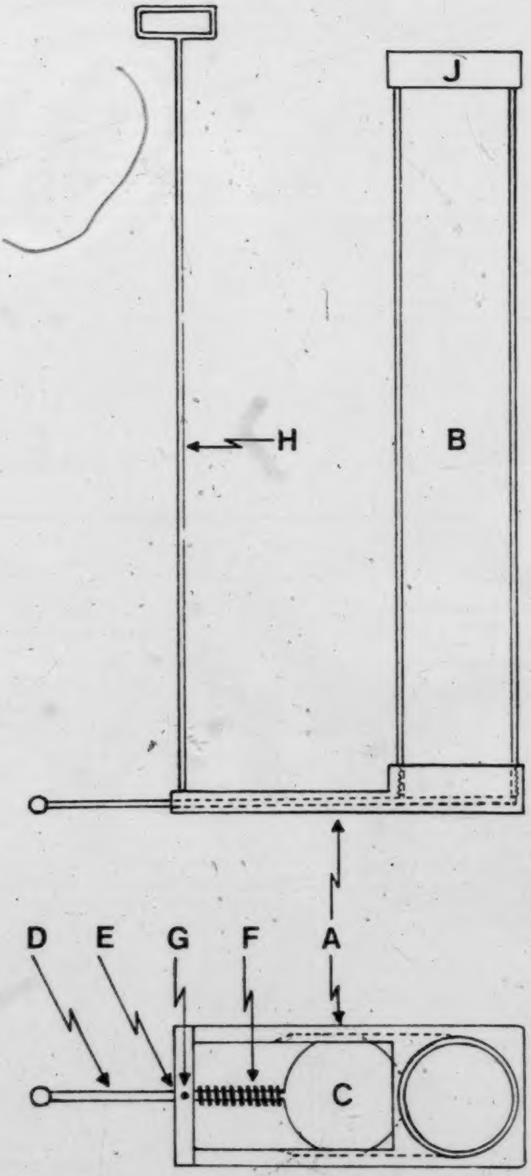

Fig. 18 Lateral and ventral views of Macrophyte Sampler A. Copied from McCauley (1975b) with permission. Different parts described in text.

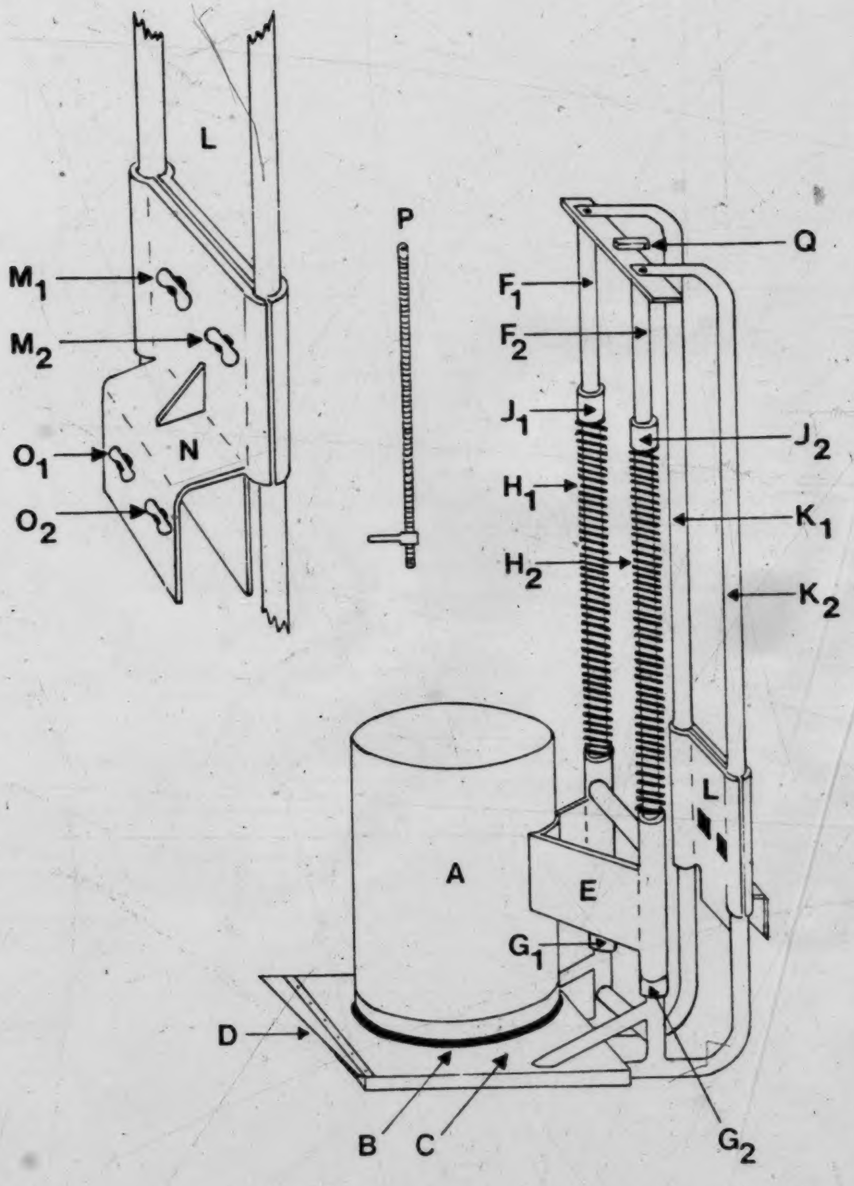
L
P
Q
M1
M2
F1
F2
J1
J2
N
O1
O2
H1
H2
K1
K2
L
A
E
G1
D
B
C
G2

Fig. 19 Macrophyte Sampler B. Copied from McCauley (1975b) with permission. Different parts described in text.

until it was about 2 cm above the mud-water interface. Cylinder A, 50 cm high and 30 cm in diameter, was then raised along pipes F_1 and F_2, compressing springs H_1 and H_2. The cylinder was held up with trigger P, which pivoted on part Q. The boat was then pushed stern first into the downstream end of a Sparganium bed. Once the sampler had been pushed sufficiently far into a bed of weeds, the trigger was released. The compressed springs then shot the cylinder downwards and against a circular strip of rubber (B) bonded to the base plate. The sampler was left in the water until all plants inside the cylinder had been removed. A net with a mesh size of 80 μ was then attached below a hole in the middle of the base plate. After removing the stopper from the hole and loosening wing bolts M_1 and M_2, the sampler was slowly lifted out of the water, causing water in the cylinder to drain through the net. The net's contents were then combined with the plants collected from the cylinder.

The two macrophyte samplers were only used in 1973. The dates of sampling and the number of samples collected of each material were as follows: Sparganium - 3 samples on June 11, July 11 and 31, Aug. 20 and Oct. 1, 4 samples on June 21. Hippuris - 3 samples on June 11 and 21, July 11 and Aug. 20, 4 samples on Oct. 1; and 5 samples on July 31; Moss - 3 samples on July 11 and 21, July 11 and 31, and Oct. 1; Algae - 3 samples on June 11, July 11 and 31, Aug. 30 and Oct. 1; Sponge - 3 samples on July 11 and 31, and Aug. 20; Wood -

3 samples on June 21, July 11 and 31, Aug. 20 and Oct. 1. Additional larvae were collected on Oct. 9 and 24, Nov. 7 and Dec. 12 from each of three *Sparganium* and three leaf samples. These samples had been kept submerged in small wire cages since Sept. 24, as described on page 22. In summary, the total number of samples collected from each of the nine microhabitats was as follows: sediment (252), *Sparganium* (32), *Potamogeton* (23), *Hippuris* (21), moss (15), filamentous algae (15), sponge (9), wood (16) and willow leaves (12). The total number of samples collected was 395. The small size of the sediment corer (15.2 cm^2) enabled me to analyze more samples from the sediment than from other substrates. The 143 non-sediment samples each contained many more larvae than any of the sediment samples, and altogether took four times as long to analyze than the 252 sediment samples.

D. Identification of the Chironomids

Individual larvae were kept in the laboratory at 15°C in glass vials containing a small amount of filtered stream water and covered with cotton gauze. Laboratory rearing of a large number of larvae in the above manner resulted in the association of the larvae, pupae and adults of 41 species of chironomids. The specimens were permanently mounted as follows:

1) The adults were dissected into the following parts: antennae, head, wings, legs of the left side, thorax

with attached right legs, and abdomen.

2) The head, thorax and abdomen were placed in 10% potassium hydroxide until the muscles were macerated.

3) All adult parts plus the larval and pupal exuviae were then passed through glacial acetic acid (10-15 min) and absolute alcohol (10-15 min).

4) The different parts were then mounted individually in Euparal and covered with small circular coverglasses.

Most of the male adults could be separated to species using the magnification of a dissecting microscope. However, male adults of Tanytarsini had to be wet mounted and the genitalia examined with a compound microscope at 100 X magnification. Larvae were either placed in 10% potassium hydroxide until the muscles in the head capsules were macerated, passed through glacial acetic acid and absolute alcohol and mounted in Euparal, or they were mounted directly in water-soluble media such as Turtox CMC-10, Aquamount, or Lactophenol.

Preliminary identifications were made referring to a large number of published papers and monographs. These are cited in Hamilton _et al_. (1969). Identifications were verified by comparing the specimens from the Bigoray River with identified specimens in the Canadian National Collection. In addition, Tanypodinae were verified by Dr. S.S. Roback, Academy of Natural Sciences of Philadelphia, Orthocladiinae were verified by Dr. D.R. Oliver, Biosystematic Institute, Ottawa, and Dr. O.A. Saether, Museum of Zoology, University of Bergen; Orthocladius by Dr. A.R. Saponis, Laboratory of Aquatic Entomology, Florida Agricultural and Mechanical University, Tallahassee; Chironomini by Dr. D.R. Oliver; and Tanytarsini by Dr. J.E. Sublette, Eastern New Mexico University, Portales. Voucher specimens have been deposited with the Canadian National Collection, Biosystematics Institute, Ottawa.

E. Calculation of Percent Overlap

A resource (e.g., space, food) can be divided into different categories (e.g., microhabitats, food types) and the percentage of a population utilizing each category can be determined to give a resource utilization curve. The percent overlap of resource utilization curves of different species can then be calculated according to the following formula:

$$\%\ \text{overlap} = \sum_{i=1}^{n} C_i$$

where C_i is the percentage occurrence common to two species in the ith resource category, and $\sum_{i=1}^{n}$ is the summation of C_i for all n resource categories. (Table VII). This formula is similar to that used by Schoener (1968). Other formulae for calculating overlap between resource utilization curves have been proposed (Ricklefs 1966, MacArthur and Levins 1967), but are all more difficult to compute than Schoener's formula.

TABLE VII Three examples showing the calculation of percent overlap between a hypothetical pair of species.

Amount of Overlap	Resource Category	% of Population in Each Category		C_i
		Sp. A	Sp. B	
None	1	60	0	0
	2	40	0	0
	3	0	50	0
	4	0	50	0
			% overlap =	0
Complete	1	30	30	30
	2	40	40	40
	3	20	20	20
	4	10	10	10
			% overlap =	100
Partial	1	30	0	0
	2	50	20	20
	3	20	60	20
	4	0	20	0
			% overlap =	40

IV RESULTS

A. Species Composition and Relative Abundance

Of the 112 species of Chironomidae found in the emergence traps in 1973 (Tables VIII-XI), nine are new to science: *Constempellina* sp. n., *Cricotopus* sp. n., *Micropsectra* sp. n., *Nanocladius* sp. n. 1, *Nanocladius* sp. n. 2, *Parakiefferiella* sp. n. 1, *Parakiefferiella* sp. n. 2, *Stempellina* sp. n. 1, and *Stempellina* sp. n. 2. *Rheotanytarsus distinctissima* is new to North America. *Pagastiella ostansa* is a new combination. Eighteen species could only be identified to genus.

Because of the difficulty of associating females with males, relative abundance of species has been expressed in terms of mean number of males emerging per square meter of stream. Figure 20 shows species abundance curves for the 112 species. The abscissa is a logarithmic scale, with the limit of each frequency class being twice as large as the preceding one. Preston (1948) called these class intervals "octaves". Species whose frequency falls exactly onto class boundaries are placed half in the frequency class on either side of the boundary.

The expected normal frequency distribution (i.e., the smooth lines in Fig. 20) is described by the equation

$$N_r = N_o e^{-0.5\ (r/s)^2}$$

where N_r is the number of species whose abundance is r octaves greater or lesser than the modal octave, N_o is the num-

TABLE VIII Species composition and abundance (males/m^2yr) of the Subfamily Tanypodinae.

1.	Larsia pallens (Coquillett)	959.8
2.	Paramerina fragilis (Walley)	291.5
3.	Ablabesmyia mallochi (Walley)	125.0
4.	Trissopelopia ogemawi Roback	122.9
5.	Arctopelopia flavifrons (Johannsen)	61.2
6.	Labrundinia pilosella (Loew)	49.1
7.	Conchapelopia dusena Roback	38.2
8.	Procladius denticulatus Sublette	22.5
9.	Zavrelimyia thryptica (Sublette)	16.4
10.	Zavrelimyia sinuosa (Coquillett)	12.2
11.	Procladius bellus (Loew)	6.9
12.	Conchapelopia cornuticaudata (Walley)	6.0
13.	Psectrotanypus florens (Johannsen)	4.5
14.	Procladius subletti Roback	3.2
15.	Procladius nietus Roback	1.3
16.	Monopelpia sp. 1	1.3
17.	Arctopelopia sp. 2	1.2
18.	Paramerina sp. 2	1.2
19.	Nilotanypus fimbriatus (Walker)	0.8
20.	Ablabesmyia sp. 2	0.6
	Total	1,725.8

TABLE IX Species composition and abundance (males/m^2/yr) of the Subfamilies Podonominae, Diamesinae and Orthocladiinae.

Subfamily Podonominae:		
1.	*Lasiodiamesa* sp.	0.6
Subfamily Diamesinae:		
1.	*Diamesa* sp.	0.6
2.	*Odontomesa* sp.	0.6
3.	*Pseudodiamesa* sp.	0.6
Subfamily Orthocladiinae:		
1.	*Corynoneura lobata* Edward	730.5
2.	*Parakiefferiella* sp. n. 1	243.4
3.	*Limnophyes folliculatus* Saether	153.1
4.	*Heterotrissocladius changi* Saether	129.9
5.	*Nanocladius* sp. n. 1	100.9
6.	*Cricotopus bicinctus* (Meigen)	85.6
7.	*Cricotopus* sp. n.	75.9
8.	*Cricotopus trifasciatus* (Meigen)	57.6
9.	*Diplocladius cultriger* Kieffer	53.0
10.	*Limnophyes spatulosus* Saether	50.1
11.	*Psectrocladius simulans* Johannsen	49.4
12.	*Eukiefferiella paucunca* Saether	40.9
13.	*Corynoneura fittkaui* Schlee	40.8
14.	*Rheocricotopus effusus* (Walker)	29.1
15.	*Orthocladius obumbratus* Johannsen	24.0
16.	*Parakiefferiella* sp. n. 2	23.5
17.	*Cricotopus varipes* Coquillet	17.2
18.	*Synorthocladius semivirens* (Kieffer)	16.7
19.	*Orthocladius tryoni* Saponis	16.4
20.	*Thienemanniella xena* Roback	13.9
21.	*Orthocladius annectens* Saether	12.2
22.	*Eukiefferiella claripennis* (Lundbeck)	11.2
23.	*Nanocladius* sp. n. 2	10.9

- continued

Table IX (cont'd)

24.	*Nanocladius altermantherae* Dendy and Sublette	10.6
25.	*Orthocladius dentifer* Brundin	10.6
26.	*Parametriocnemus lundbecki* (Johannsen)	9.8
27.	*Rheocricotopus eminellobus* Saether	7.8
28.	*Cricotopus sylvestris* (Fabricus)	7.2
29.	*Brillia flavifrons* (Johannsen)	6.6
30.	*Limnophyes nudiradius* Saether	6.3
31.	*Limnophyes scapellatus* Brundin	6.3
32.	*Corynoneura scutulata* Winnertz	6.0
33.	*Psectrocladius flavus* Johannsen	3.7
34.	*Nanocladius* sp. 4	3.1
35.	*Acricotopus lucidus* (Staeger)	2.5
36.	*Orthocladius smolandicus* Brundin	1.4
37.	*Diplocladius bilobatus* Brundin	1.3
38.	*Prosmittia jemlandica* (Brundin)	0.8
39.	*Corynoneura coronata* Edward	0.6
40.	*Corynoneura* sp. 5	0.6
41.	*Psectrocladius semicirculatus* Saether	0.6
42.	*Smittia* sp. 1	0.6
43.	*Metriocnemus* sp. 1	0.6
44.	*Orthocladius mallochi* Kieffer	0.6
	Total	2,076.1

TABLE X Species composition and abundance (males/m^2/yr) of the Subfamily Chironomidae, Tribe Chrionomini.

1.	Paralauterborniella nigrohalterale (Townes)	352.3
2.	Pagastiella ostansa (Webb) n. comb.	249.1
3.	Polypedilum (P.) braseniae (Leathers)	73.3
4.	Cryptotendipes casuaria (Townes)	72.8
5.	Paratendipes albimanus (Meigen)	72.5
6.	Paracladopelma undine (Townes)	65.4
7.	Microtendipes pedellus (De Geer)	57.7
8.	Polypedilum (Tripodura) scalaenum (Schrank)	49.3
9.	Polypedilum (P.) fallax (Johannsen)	19.4
10.	Cryptochironomus scimitarus Townes	13.8
11.	Polypedilum (Tripodura) gomphus Townes	11.9
12.	Phaenopsectra (P.) flavipes (Meigen)	9.8
13.	Parachironomus sp.	8.6
14.	Phaenopsectra (Tribelos) jucundus (Walker)	7.2
15.	Cryptotendipes sp.	5.8
16.	Polypedilum (P.) aviceps Townes	5.2
17.	Stenochironomus taeniapennis (Coquillett)	5.0
18.	Cryptochironomus blarina Townes	3.3
19.	Paracladopelma amphitrite (Townes)	2.6
20.	Polypedilum (P.) sp. 4	2.3
21.	Dicrotendipes modestus (Say)	1.4
22.	Xenochironomus xenolabis (Kieffer)	1.2
23.	Harnischia sp.	0.6
	Total	1,090.5

TABLE XI Species composition and abundance (males/m^2/yr) of the Subfamily Chironominae, Tribe Tanytarsini.

1.	Tanytarsus dispar Lindeberg	1,481.6
2.	Stempellina leptocelloides Webb	1,073.7
3.	Rheotanytarsus distinctissima (Brundin)	426.9
4.	Tanytarsus limneticus Sublette	330.2
5.	Stempellina sp. n. 2	157.1
6.	Stempellina sp. n. 1	85.2
7.	Tanytarsus curticornis Kieffer	58.2
8.	Micropsectra polita (Malloch)	44.7
9.	Micropsectra attenuata Reiss	23.4
10.	Paratanytarsus dissimilis (Johannsen)	23.1
11.	Micropsectra dubia (Malloch)	15.0
12.	Tanytarsus anderseni Reiss and Fittkau	4.4
13.	Tanytarsus buckleyi Sublette	4.2
14.	Cladotanytarsus viridiventris (Malloch)	3.5
15.	Micropsectra sp. n.	3.2
16.	Tanytarsus debilis (Meigen)	1.5
17.	Tanytarsus sp. 7	1.3
18.	Paratanytarsus sp. 2	1.3
19.	Tanytarsus confusus Malloch	0.6
20.	Constempellina sp. n.	0.6
21.	Micropsectra xantha Roback	0.6
	Total	3,740.3

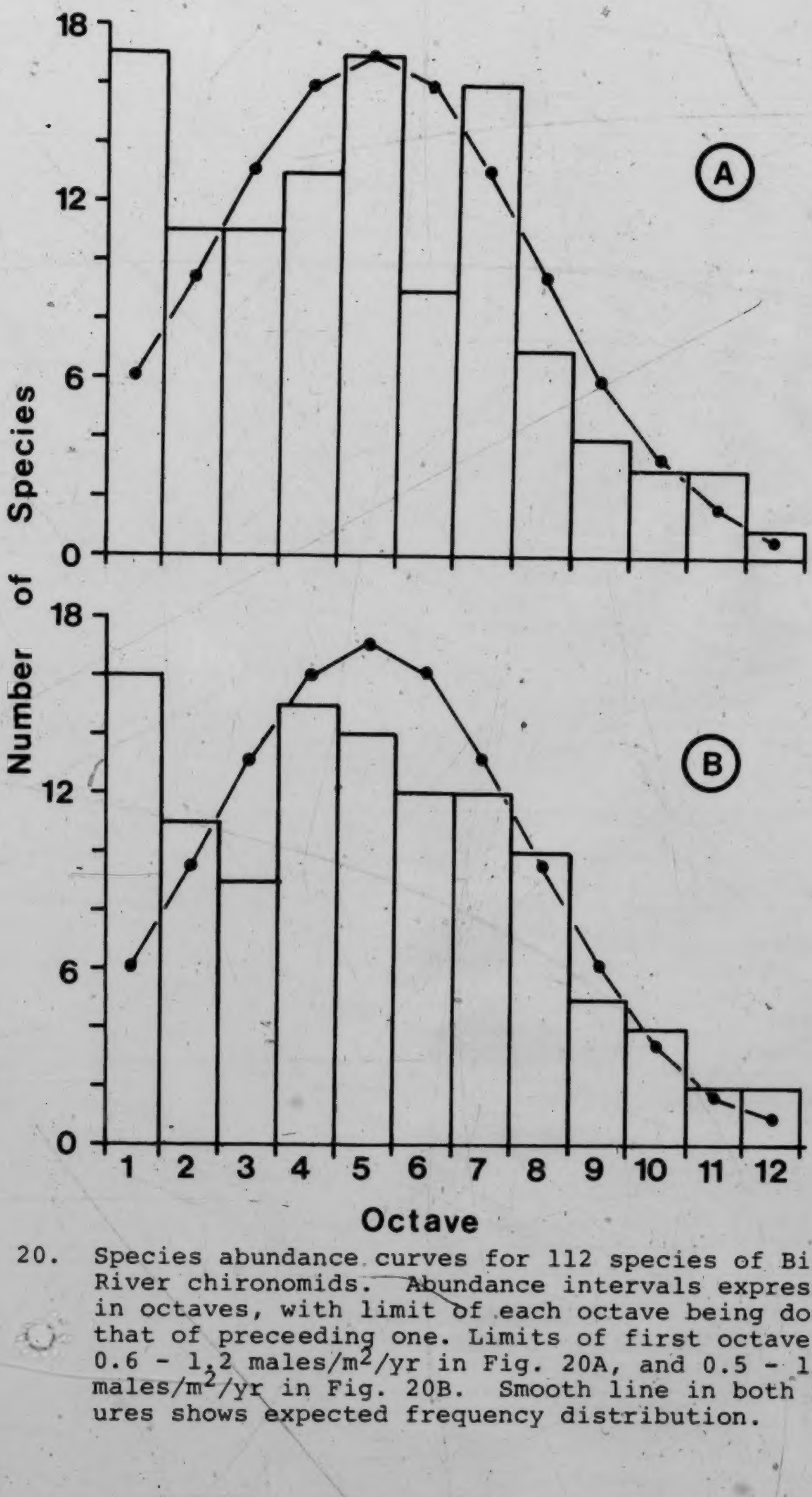

Fig. 20. Species abundance curves for 112 species of Bigoray River chironomids. Abundance intervals expressed in octaves, with limit of each octave being double that of preceeding one. Limits of first octave are 0.6 - 1.2 males/m^2/yr in Fig. 20A, and 0.5 - 1.0 males/m^2/yr in Fig. 20B. Smooth line in both figures shows expected frequency distribution.

ber of species in the modal octave, and s is the standard deviation of the observed frequency distribution. The standard deviation is 2.8 for both Figures 20A and 20B, and the fitted curves are described by the equation

$$N_r = 17_e{}^{-0.5\ (r/2.8)^2}$$

The greatest discrepancy between the observed and expected frequency distributions occurs in the first octave (i.e., in the number of very rare species). If the first octave is excluded, then the observed and expected frequencies do not differ significantly (for Fig. 20A, $\chi^2 = 6.47$, 8 d.f., $p = 0.5$-0.7; for Fig. 20B, $\chi^2 = 9.26$, 8 d.f., $p = 0.8$-0.9). When the first octave is included in the comparison, then the differences between the expected and observed frequency distributions are significant (for Fig. 20A, $\chi^2 = 25.95$, 9. d.f., $p<0.01$; for Fig. 20B, $\chi^2 = 20.33$, 9 d.f., $p = 0.01$-0.02).

The fitted normal curve is symmetrical about the modal octave, but is truncated on the left (the so-called "veil line") because a number of very rare species were missed in the survey. The total number of species which theoretically could be present in the community can be estimated by the equation $N = 2.5\ s\ N_o$, where s and N_o are as described above. Since $s = 2.8$ and $N_o = 17$, the total theoretical number of species in the study area is 119. The 112 species found in the present survey therefore constitute 94%

of the number theoretically present.

In the Bigoray River the percent abundance of the four major taxonomic groups (subfamilies Tanypodinae and Orthocladiinae, and tribes Chironomini and Tanytarsini of the subfamily Chironominae) was as follows:

	Tanyp.	Ortho.	Chiro.	Tanyt.
By number of individuals				
Males and females	20	19	12	49
Males only	20	24	13	43
By number of species	18	43	20	19

B. Seasonal Patterns of Emergence

In 1973, the first chironomids emerged during the third sampling interval (May 3-8) when the mean daily water temperature had risen to 7 °C (Fig. 21). The last chironomids emerged during the 35th sampling interval (Sept. 24-Oct. 1) when the water temperature was 8°C. The total length of the emergence season (middle of third sampling interval to middle of 35th sampling interval) was 140 days. During this time, an average of 19.3×10^3 chironomids emerged per square meter of stream. The maximum daily emergence rate, 573 chironomids/m^2/day, occurred during the 25th sampling interval (July 31-Aug. 4). Increases in water level and decreases in water temperature reduced the daily emergence rate. During long periods of rainy, cool weather, such as occurred during 1971 and 1972, emergence stopped completely.

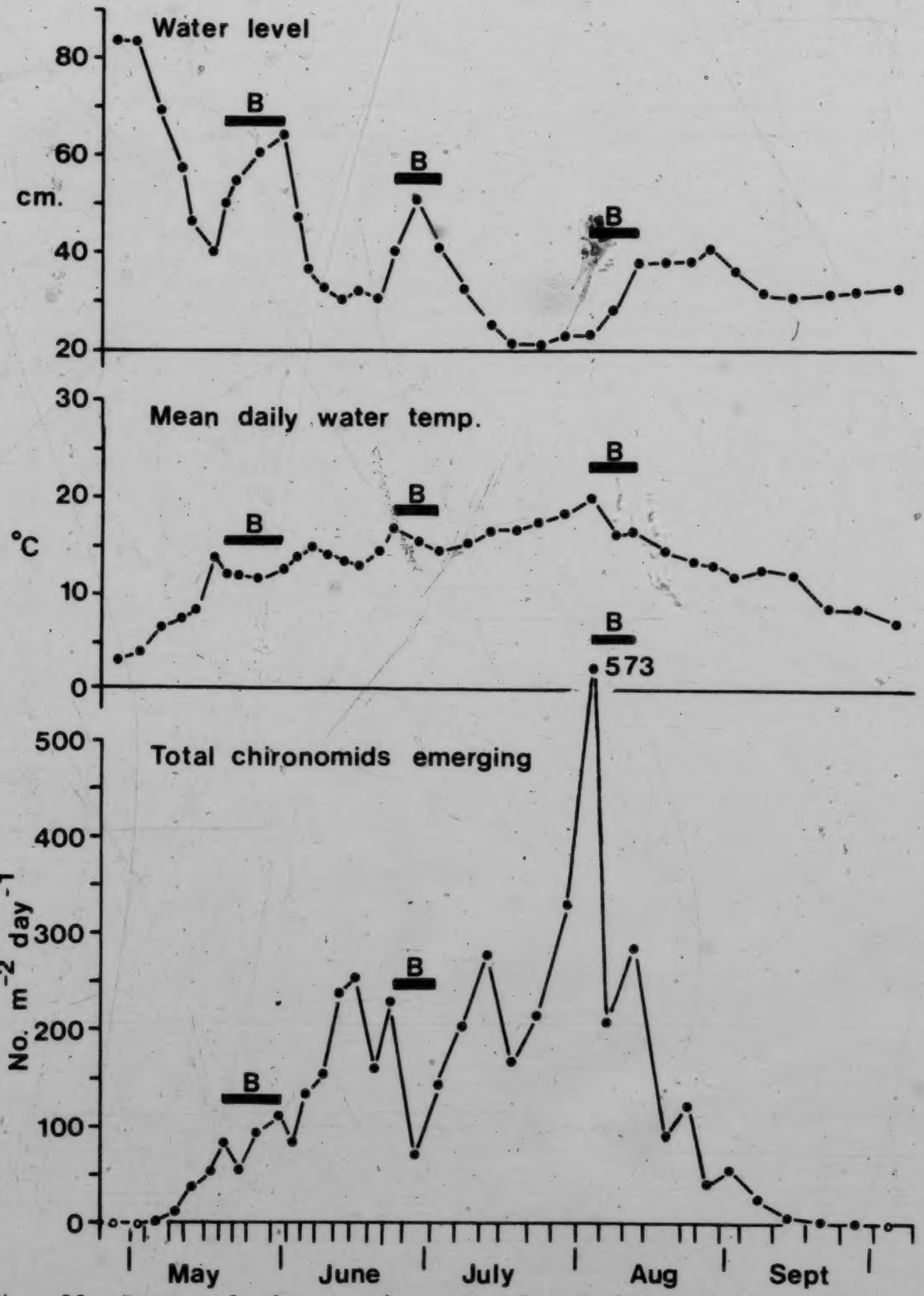

Fig. 21 Seasonal changes in water level, mean daily water temperature, and mean daily emergence rate of chironomids in the Bigoray River during 1973. B indicates cool, rainy periods. Open circles indicate no emergence.

Orthocladiinae were the most abundant group at the start and end of the emergence season (Fig. 22). This is not surprising since the Orthocladiinae are the most cold-adapted group among the Chironomidae (Thienemann 1954, Oliver 1971). Tanypodinae were most abundant group near the middle of the emergence season, whereas Tanytarsini reached peaks of abundance between those of Othocladiinae and Tanypodinae. Maximum water temperature occurred during the second period of peak emergence of Tanytarsini. Chironomini were most abundant group only during the 19th sampling interval (July 1-6), and then only by a small amount. The subfamilies Podonominae and Diamesinae were insignificant both in number of species and number of individuals (Table IX).

Seasonal changes in emergence rates of the 32 most abundant species (i.e., those with a yearly emergence of 50 males/m^2 or more) are shown in Figures 23-29. The same data are shown in Figures 30-33 in the form of cumulative emergence curves. From these, one can easily determine the dates when 25%, 50% and 75% of a species' emergence had occurred. Additional emergence statistics are given in Table XII. The length of a species' emergence period includes only those days that the species was actually found emerging. Emergence periods varied from 15 days (Diplocladius cultriger) to 122 days (Limnophyes folliculatus), with the average length being 67 days. The mean length for all 32 emergence periods was

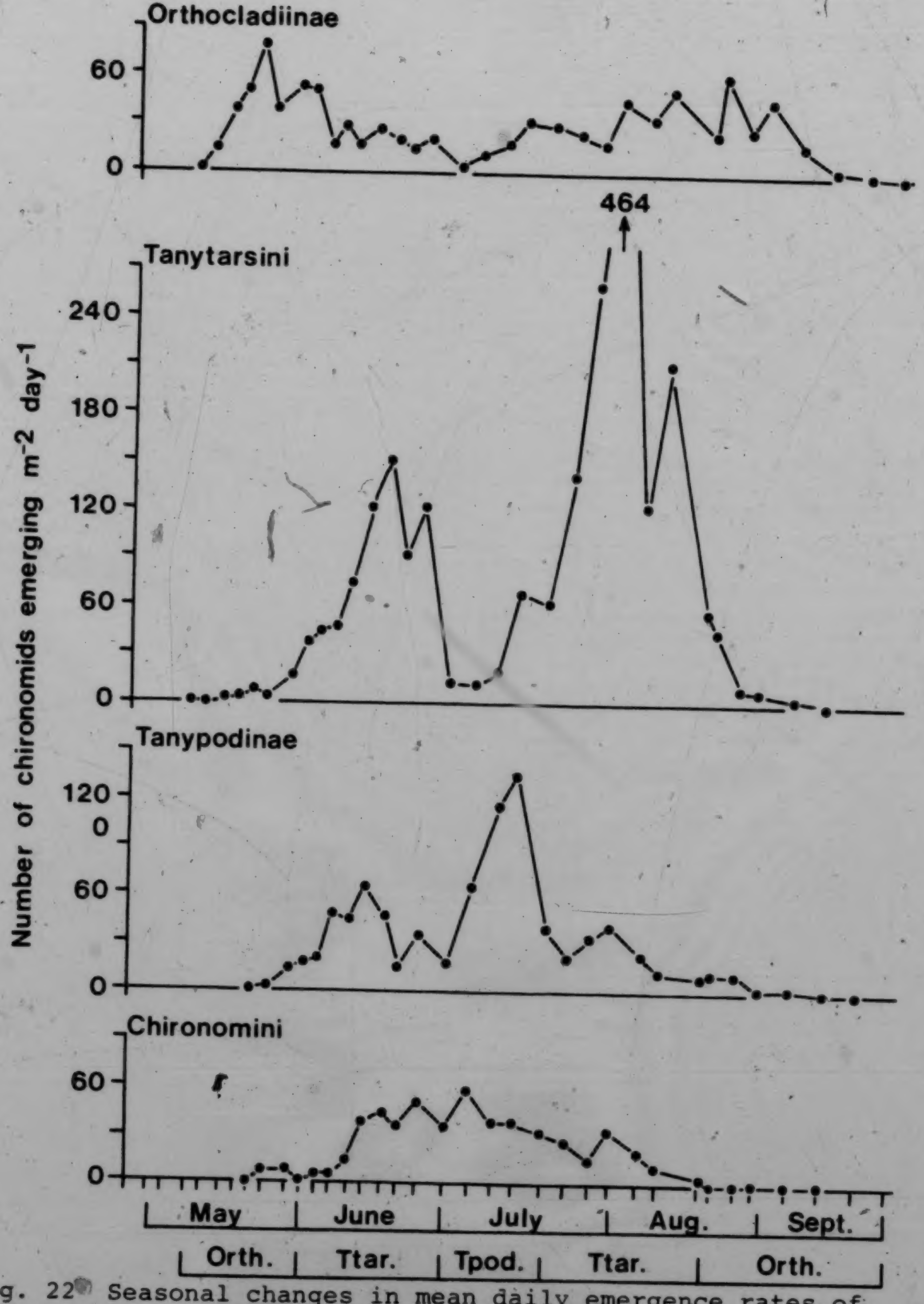

Fig. 22 Seasonal changes in mean daily emergence rates of Orthocladiinae, Tanytarsini, Tanypodinae and Chironomini in the Bigoray River during 1973. Periods when a particular group predominated are shown at bottom of figure.

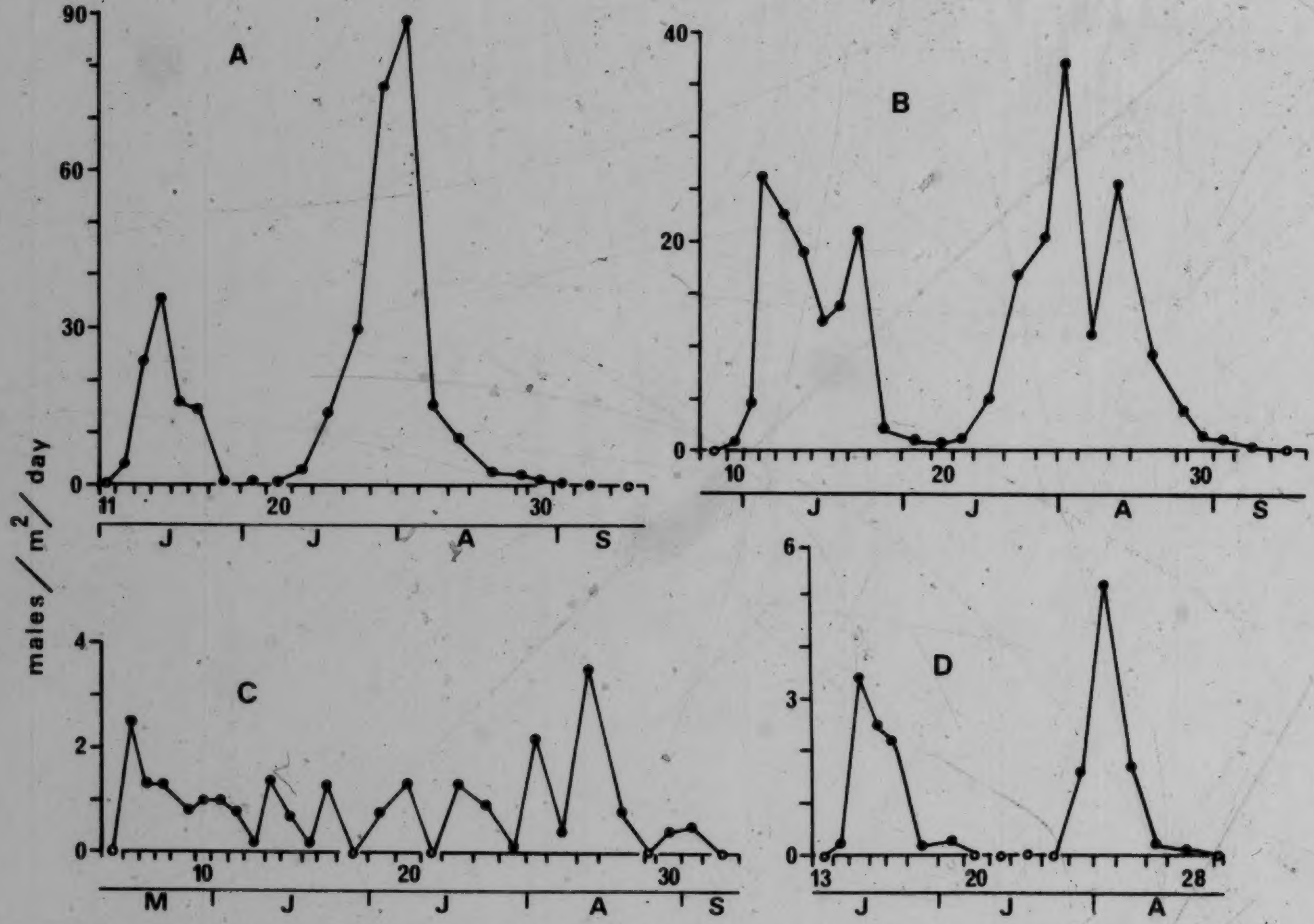

Fig. 23 Seasonal changes in mean daily emergence rates of *Tanytarsus dispar* (A), *Stempellina leptocelloides* (B), *Nanocladius* sp.n. 1 (C), and *Polypedilum braseniae* (D) in the Bigoray River during 1973. In Fig. 23-29, numbers along abscissa indicate sampling intervals, and open circles indicate no emergence.

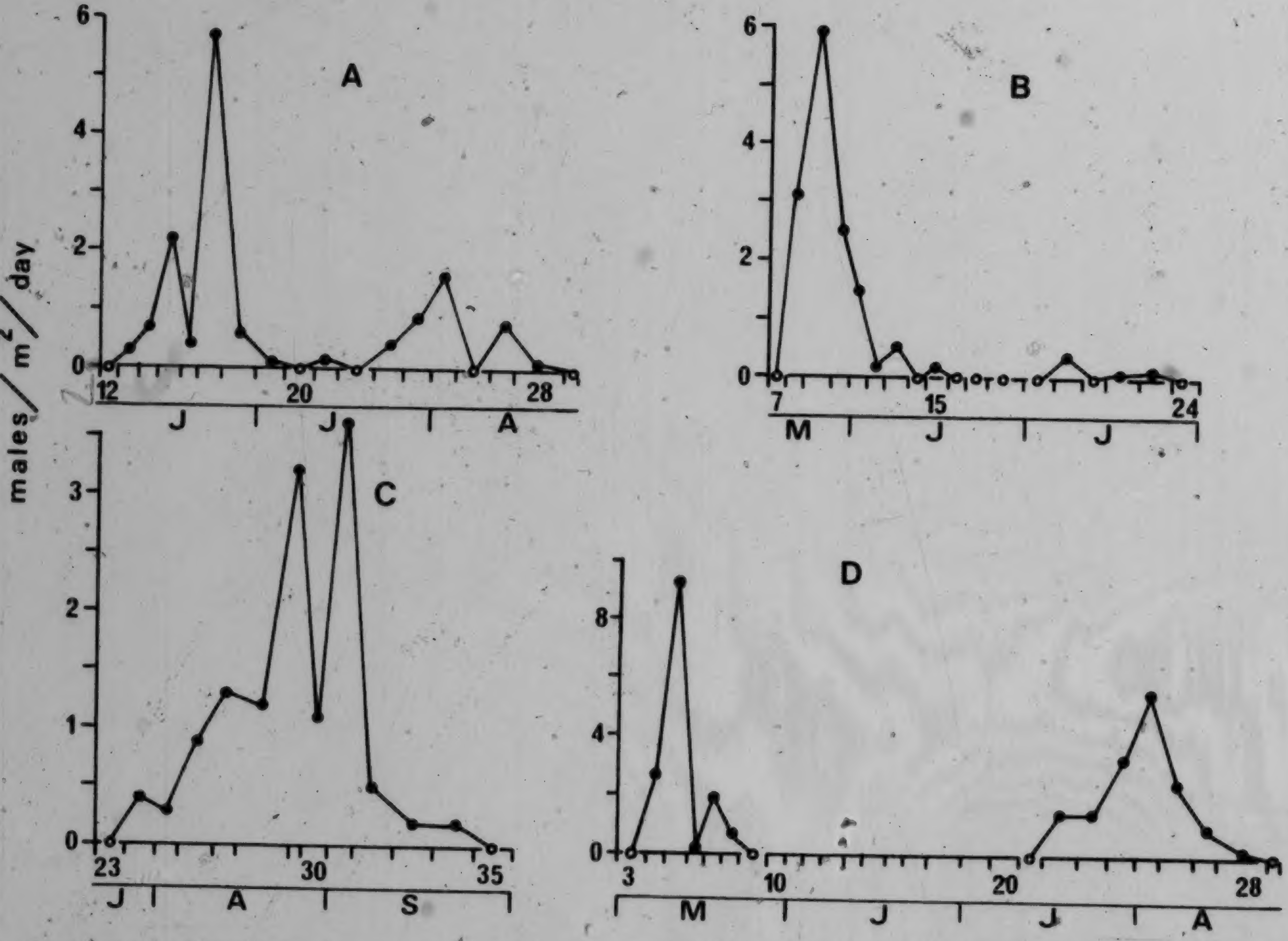

Fig. .24 Seasonal changes in mean daily emergence rates of *Tanytarsus curticornis* (A) *Microtendipes pedellus* (B), *Cricotopus sylvestris* (C), and *Heterotrissocladius changi* (D) in the Bigoray River during 1973.

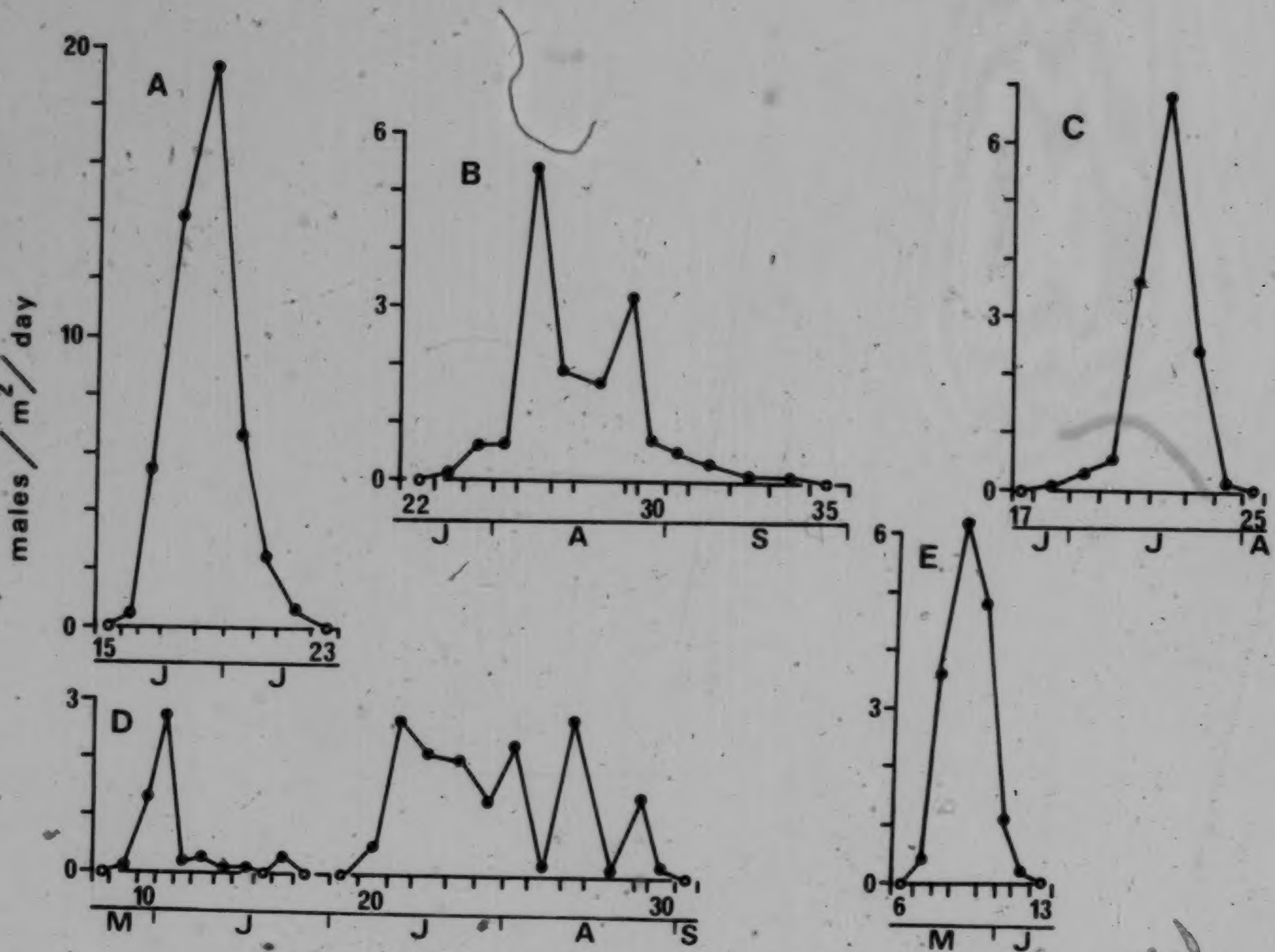

Fig. 25 Seasonal changes in mean daily emergence rates of Pagastiella ostansa (A) Cricotopus sp.n. (B), Paratendipes albimanus (C), Stempellina sp.n. 1 (D) and Arctopelopia flavifrons (E) in the Bigoray River during 1973.

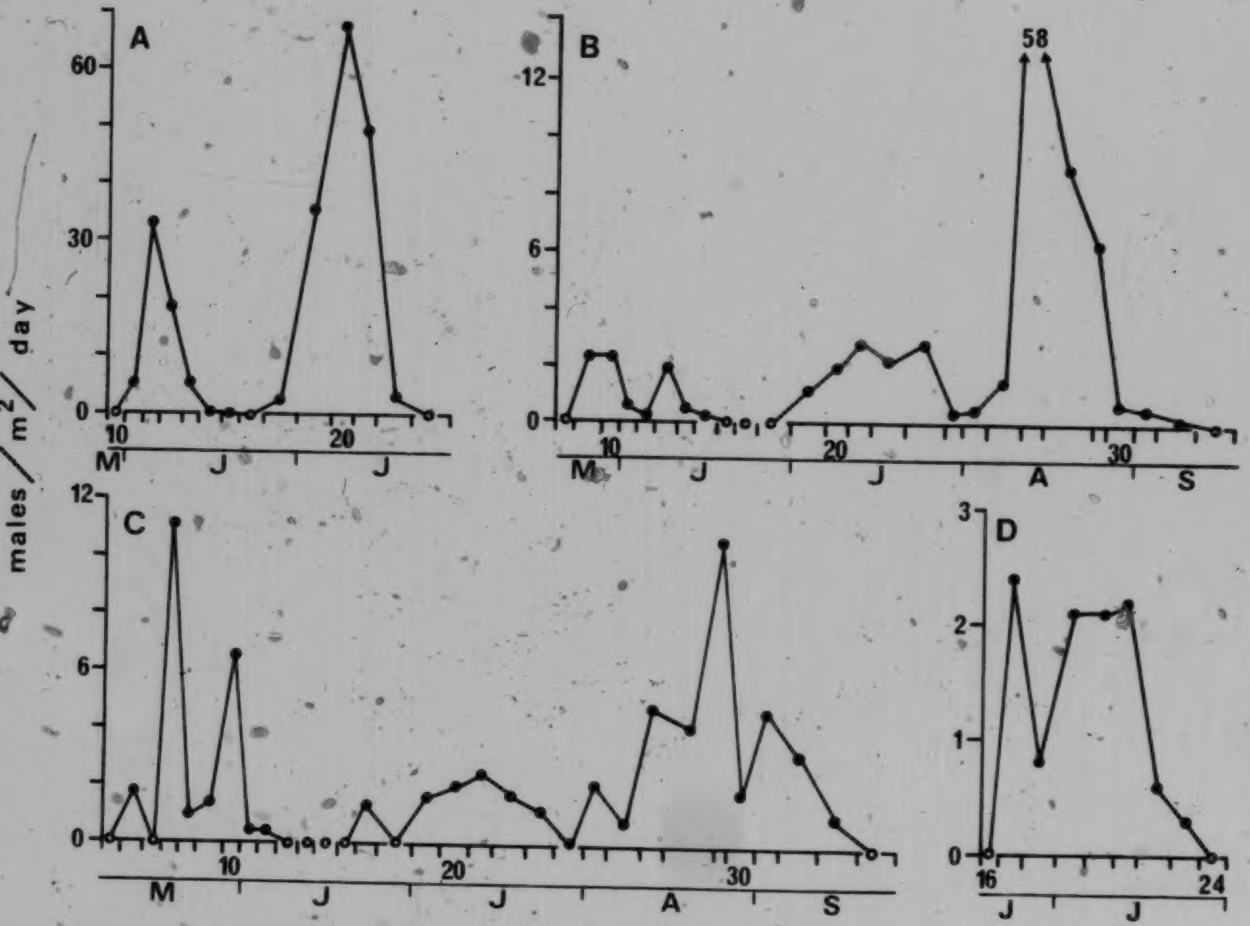

Fig. 26 Seasonal changes in mean daily emergence rates of *Larsia pallens* (A), *Rheotanytarsus distinctissima* (B), *Corynoneura lobata* (C), and *Polypedilum scalaenum* (D) in the Bigoray River during 1973.

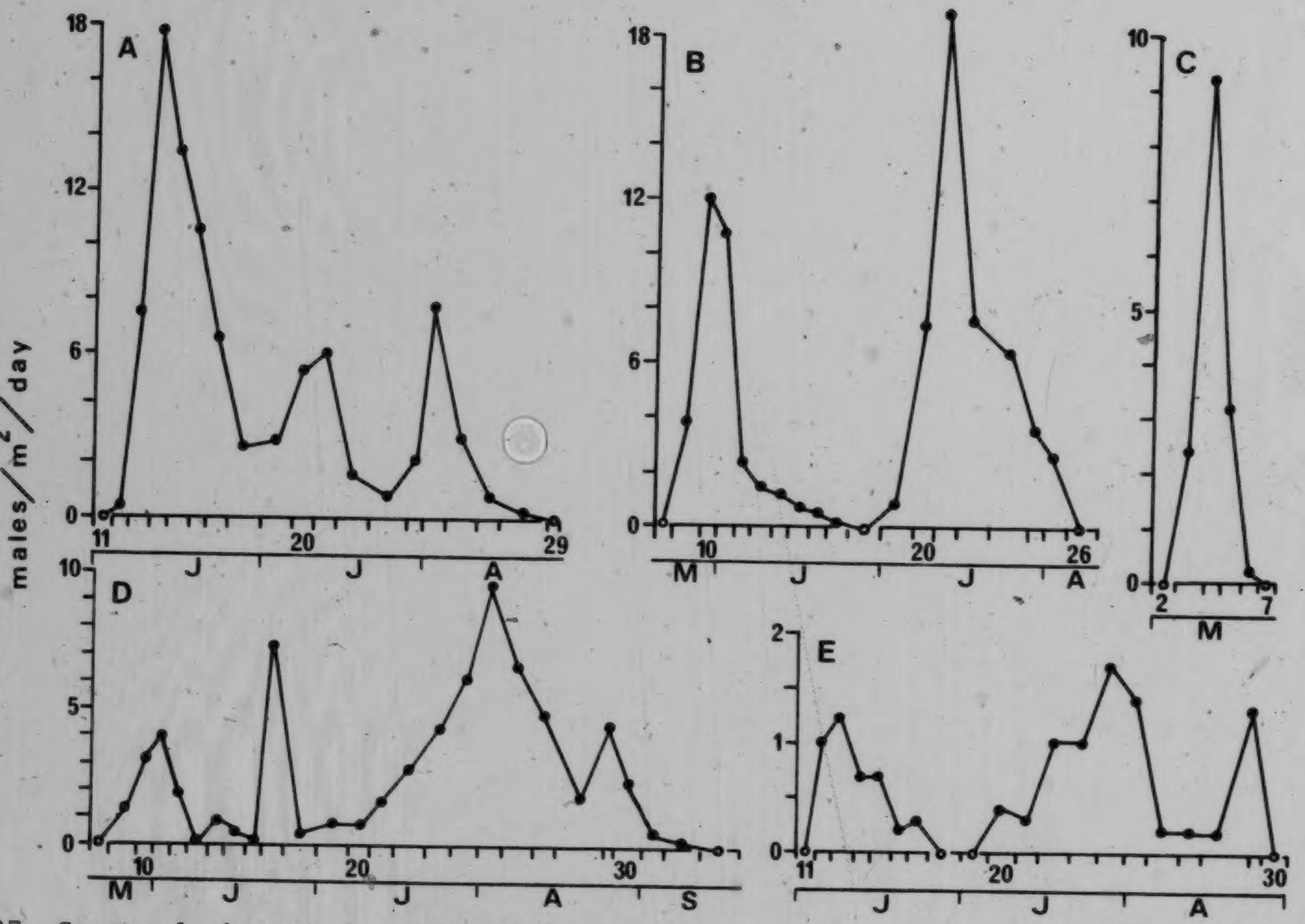

Fig. 27 Seasonal changes in mean daily emergence rates of *Paralauterborniella nigrohalterale* (A), *Tanytarsus limneticus* (B), *Diplocladius cultriger* (C), *Paramerina fragilis* (D), and *Labrundinia pilosella* (E) in the Bigoray River during 1973.

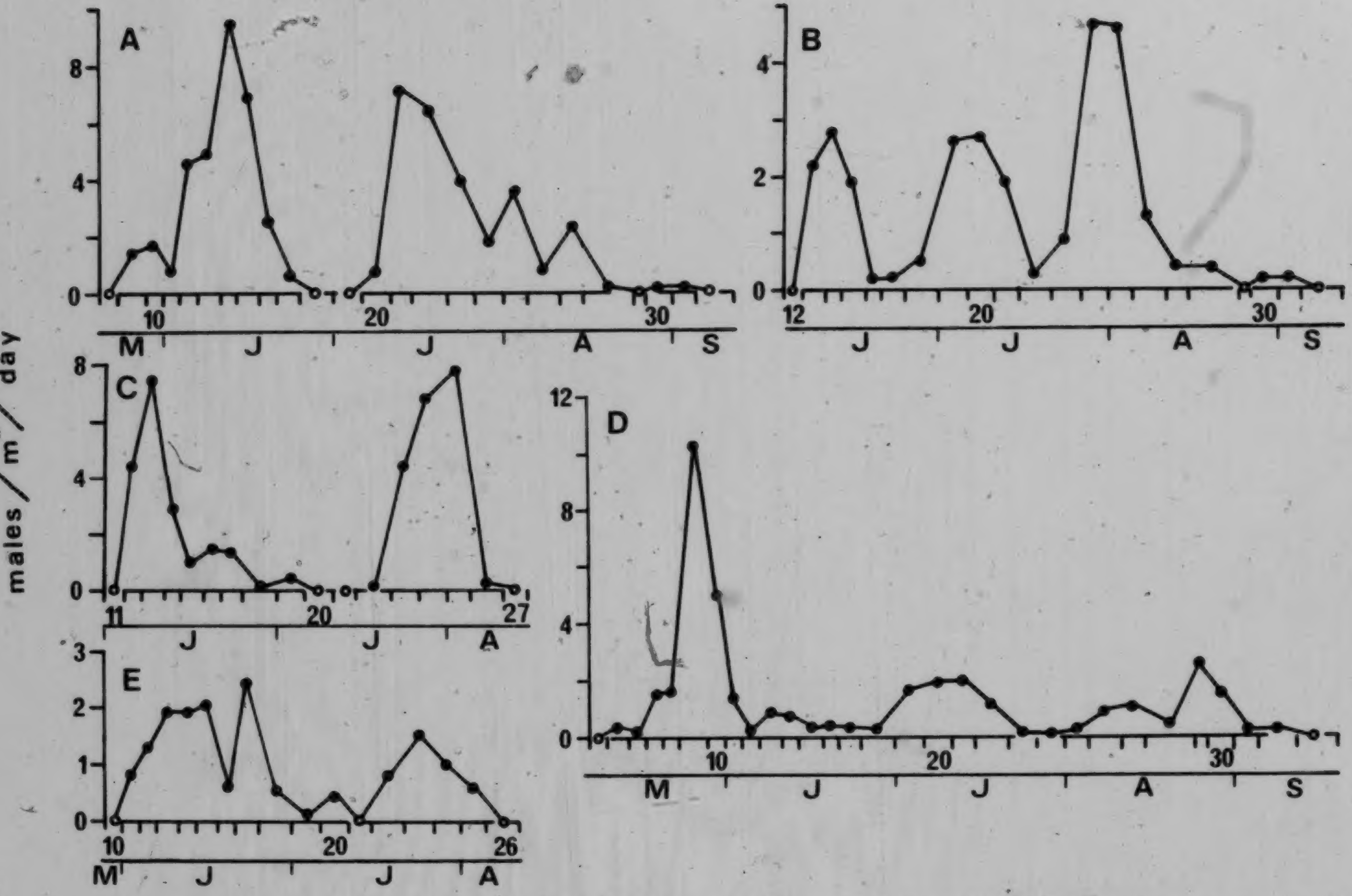

Fig. 28 Seasonal changes in mean daily emergence rates of Parakiefferiella sp.n. 1 (A), Ablabesmyia mallochi (B), Stempellina sp.n. 2 (C), Limnophyes folliculatus (D), and Paracladopelma undine (E) in the Bigoray River during 1973.

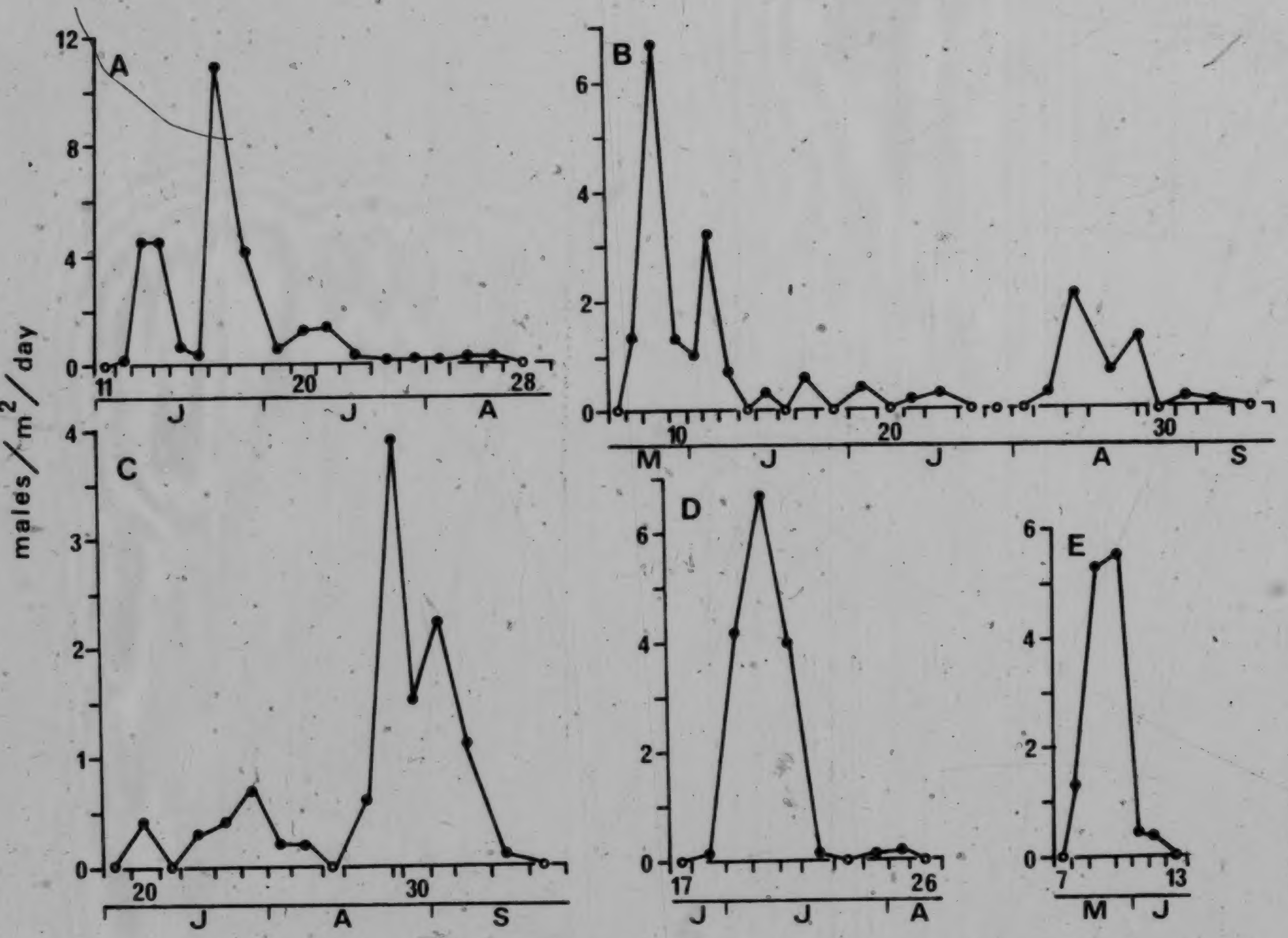

Fig. 29 Seasonal changes in mean daily emergence rates of Trissopelopia ogemawi (A), Cricotopus bicinctus (B), Psectrocladius simulans (C), Cryptotendipes casuaria (D), and Limnophyes spatulosus (E) in the Bigoray River during 1973.

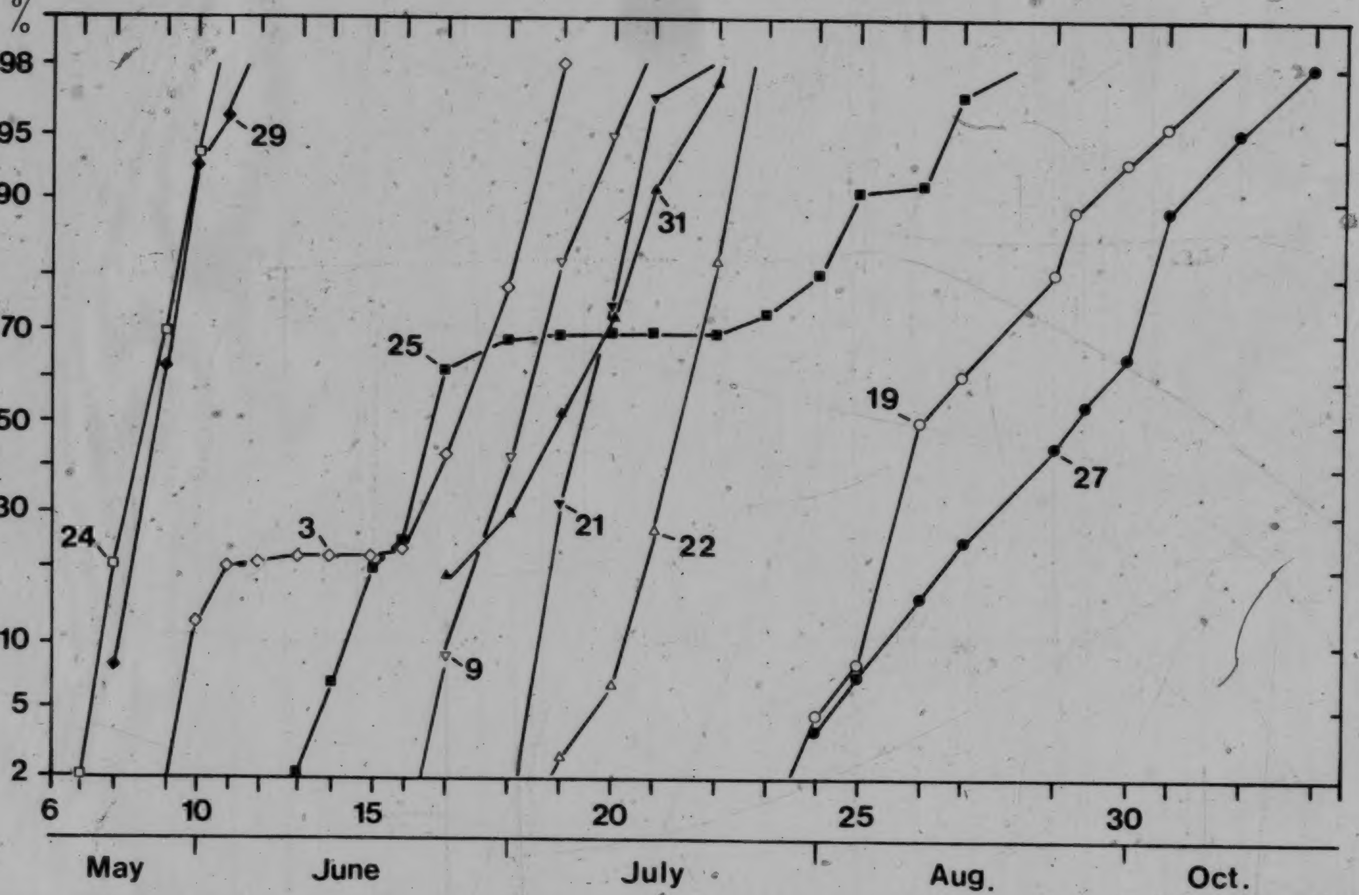

Fig. 30 Cumulative emergence curves for *Larsia pallens* (3), *Pagastiella ostensa* (9), *Cricotopus* sp. n. (19), *Cryptotendipes casuaria* (21), *Paratendipes albimanus* (22), *Arctopelopia flavifrons* (24), *Tanytarsus curticornis* (25) *Cricotopus trifasciatus* (27) *Limnophyes spatulosus* (29), and *Polypedilum scalaenum* (31). In Figs. 30 - 33, sampling interval numbers are given along abscissa, and percent emergence is given along ordinate.

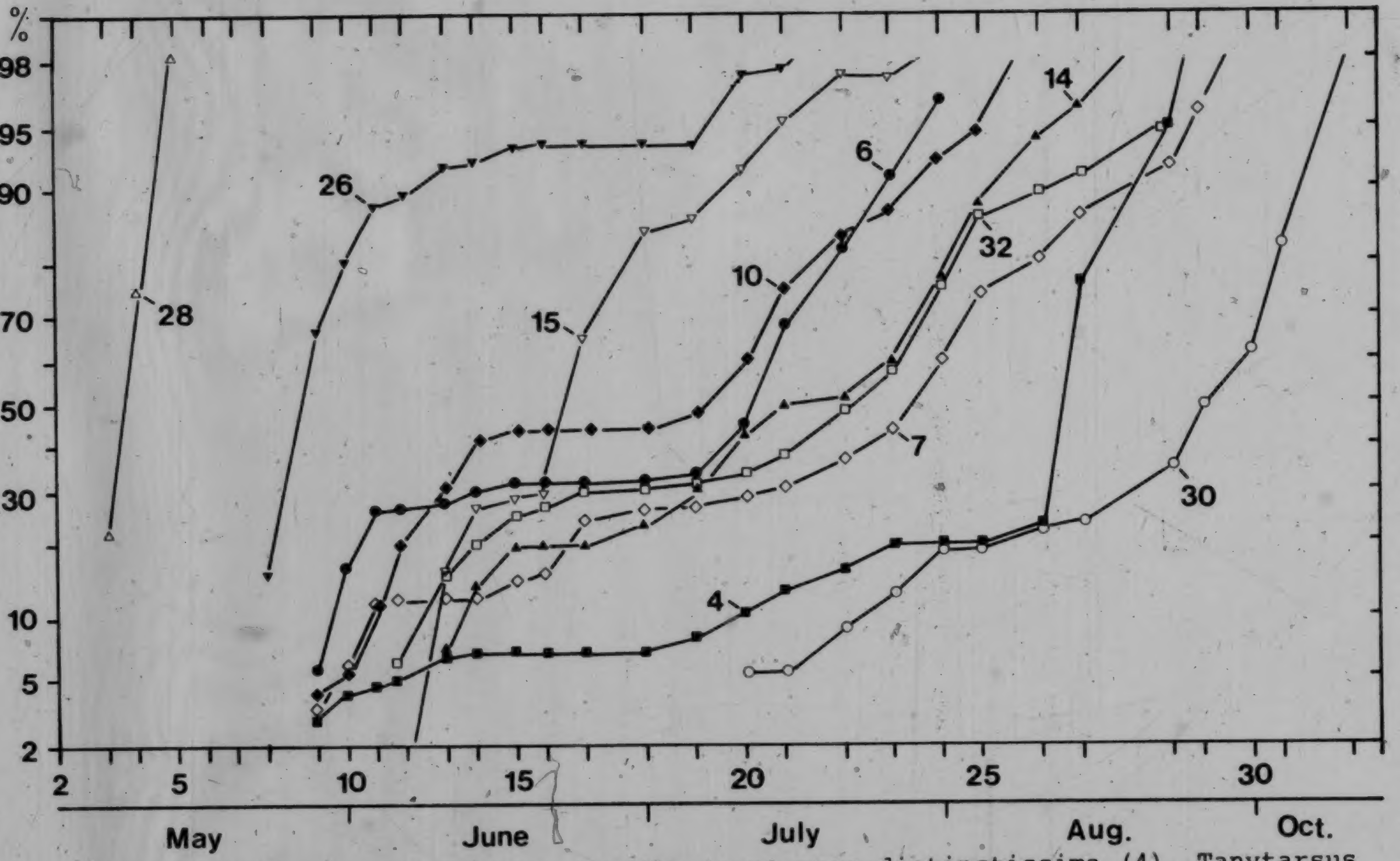

Fig. 31 Cumulative emergence curves for *Rheotanytarsus distinctissima* (4), *Tanytarsus limneticus* (6), *Paramerina fragilis* (7), *Parakiefferiella* sp.n. 1 (10), *Ablabesmyia mallochi* (14), *Trissopelopia ogemawi* (15), *Microtendipes pedellus* (26), *Diplocladius cultriger* (28), *Psectrocladius simulans* (3), and *Labrundinia pilosella* (32).

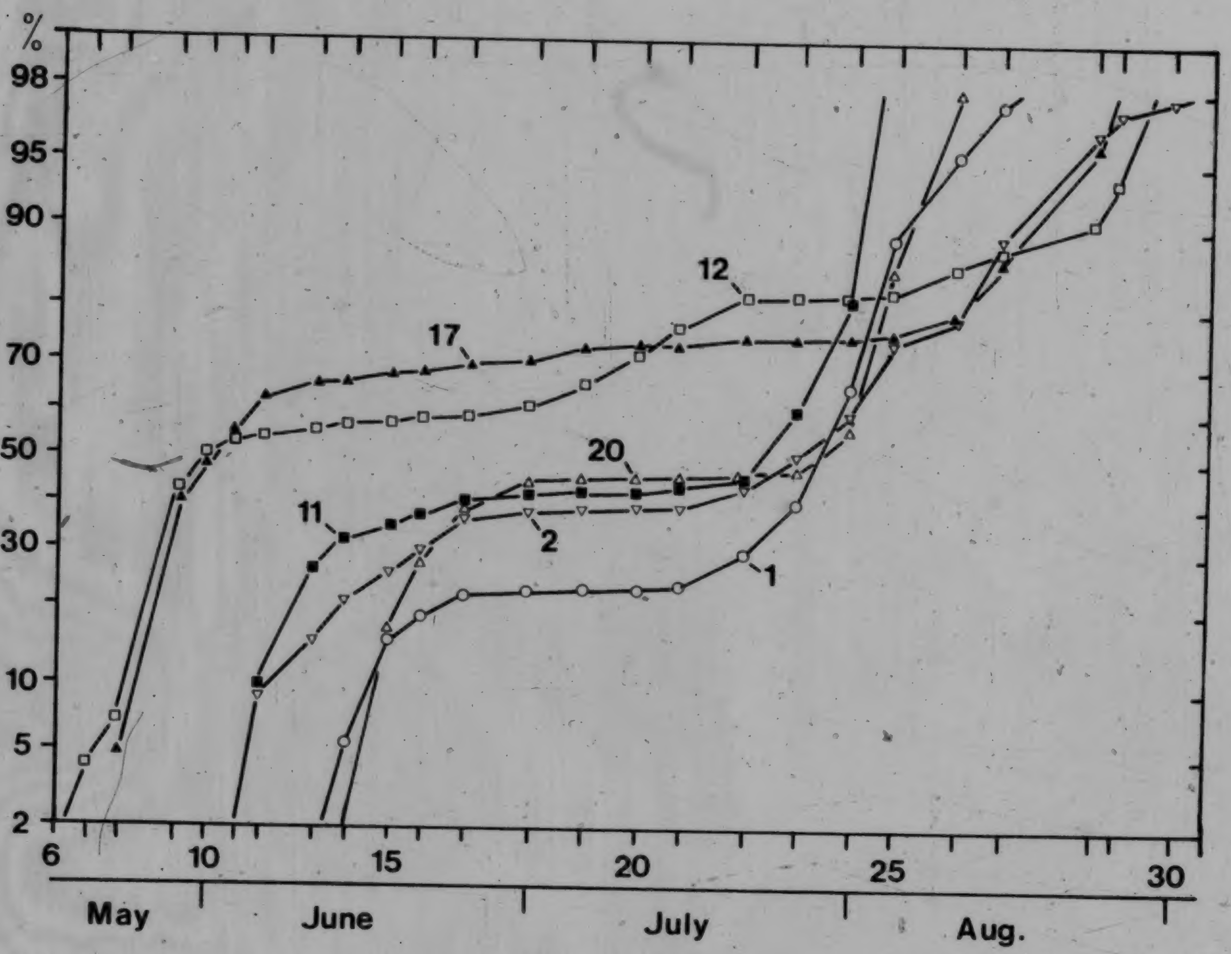

Fig. 32 Cumulative emergence curves for Tanytarsus dispar (1), Stempellina leptocelloides (2), Stempellina sp.n. 2 (11), Limnophyes folliculatus (12), Cricotopus bicinctus (17), and Polypedilum braseniae (20).

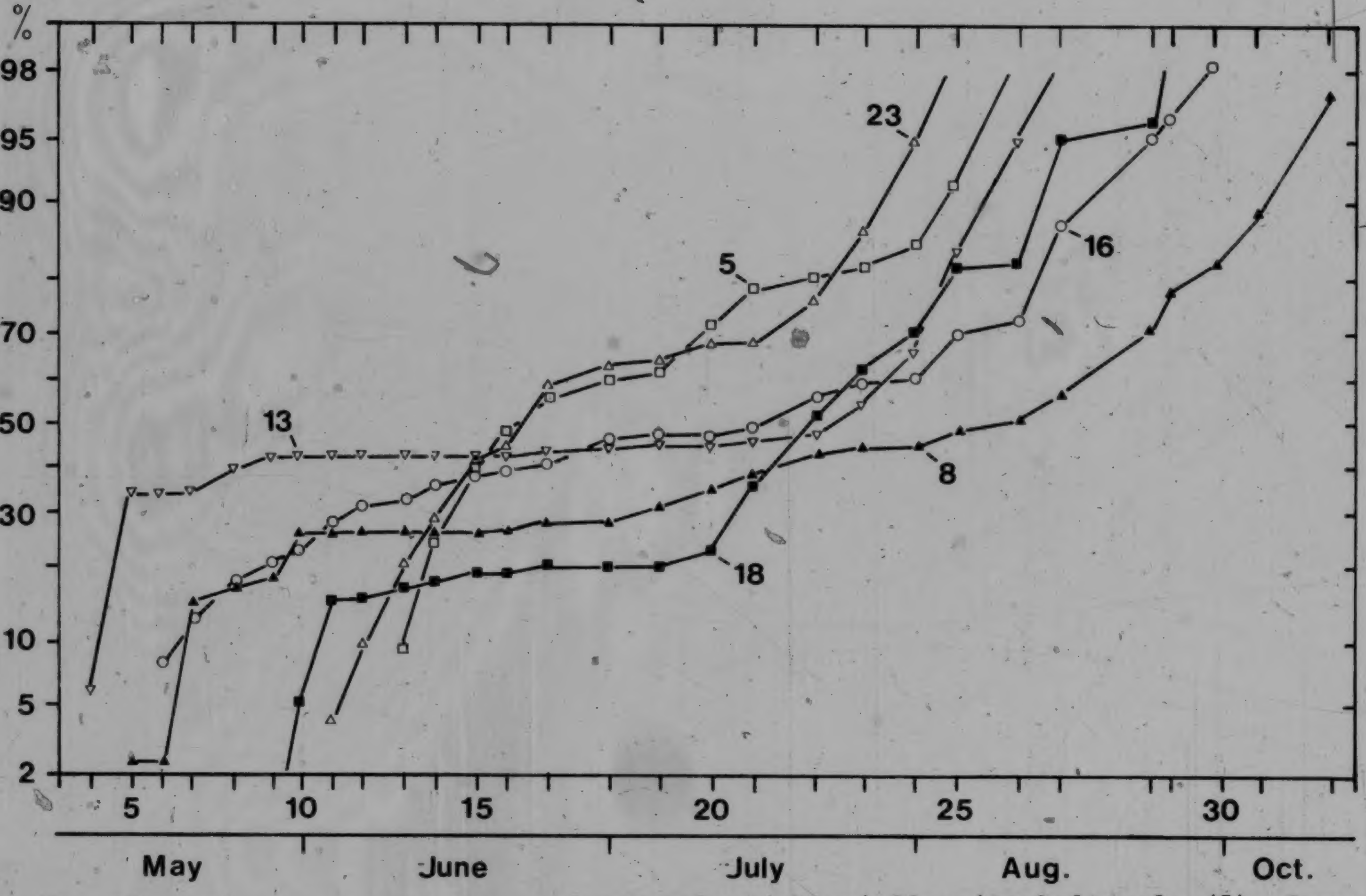

Fig. 33 Cumulative emergence curves for *Paralauterborniella nigrohalterale* (5), *Corynoneura lobata* (8), *Heterotrissocladius changi* (13), *Nanocladius* sp.n. 1 (16) *Stempellina* sp.n. 1 (18), and *Paracladopelma undine* (23).

TABLE XII Summary of emergence statistics for 32 commonest chironomid species in the Bigoray River. Statistics explained in text. Species arranged in order of decreasing abundance.

Species	Length (days)	H' (bits)	No. of phases	Mean % overlap	Ratio M:F
Tanytarsus dispar	109	3.06	2	30	-
Stempellina leptocelloides	107	3.91	2	35	-
Larsia pallens	49	2.49	2	18	1.0
Rheotanytarsus distinctissimus	96	2.41	3	20	-
Paralauterborniella nigrohalterale	80	3.60	3	30	0.7**
Tanytarsus limneticus	77	3.29	2	31	-
Paramerina fragilis	109	3.92	3	36	0.6**
Corynoneura lobata	106	4.03	3	26	0.6**
Pagastiella ostansa	33	1.61	1	16	-
Parakiefferiella sp.n.1	82	3.68	2	31	0.5**
Stempellina sp.n.2	58	2.93	2	25	-
Limnophyes folliculatus	122	3.67	3	29	0.7**
Heterotrissocladius changi	55	3.04	2	23	0.7**
Ablabesmyia mallochi	86	3.46	3	33	0.7**
Trissopelopia ogemawi	67	2.78	1	22	1.1
Nanocladius sp.n.1	94	4.06	?	31	0.8*
Cricotopus bicinctus	76	3.10	2	25	0.6**
Stempellina sp.n.1	84	3.44	2	33	-

- continued

Table XII (cont'd)

Species	Length (days)	H' (bits)	No. of phases	Mean % overlap	Ratio M:F
Cricotopus sp.n.1	65	2.53	1	17	1.3
Polypedilum braseniae	53	2.83	2	23	0.8
Cryptotendipes casuaria	35	1.71	1	14	-
Paratendipes albimanus	31	1.73	1	15	0.4**
Paracladopelma undine	69	3.53	2	31	0.5**
Arctopelopia flavifrons	20	1.76	1	13	0.5**
Tanytarsus curticornis	67	2.90	2	26	-
Microtendipes pedellus	41	2.30	2	18	1.6**
Cricotopus trifasciatus	63	3.10	1	17	0.9
Diplocladius cultriger	15	1.54	1	1	2.1**
Limnophyes spatulosus	22	1.61	1	13	1.0
Psectrocladius simulans	69	3.25	2	19	1.2
Polypedilum scalaenum	35	2.55	1	21	0.6**
Labrundinia pilosella	71	3.67	2	35	0.6**
Means	67	2.92	1.8	24	0.8**

* Significantly different from 1.0 at the 5% level.

** Significantly different from 1.0 at the 1% level.

67 days, or about half the length of the emergence season (140 days).

The diversity (H') of a species' emergence period was calculated using the Shannon-Wiener diversity index

$$H' = -1.44 \sum_{i=1}^{n} p_i \log_e p_i$$

where p_i is the proportion of the individuals of a species emerging in the ith sampling interval. The diversity value combines information on both the length of the emergence period and on the constancy of the emergence rate throughout the emergence period. A species with a long emergence period generally had a higher emergence diversity than a species with a shorter emergence period ($r = 0.85$, $p<0.01$). If the length of the emergence period of two species is the same, then the species with the most uniform emergence rate throughout the emergence period will have the greatest emergence diversity. This can be illustrated by comparing the emergence graph of _Cryptotendipes casuaria_ (Fig. 29D) with that of _Polypedilum scalaenum_ (Fig. 26D). Both species have an emergence period of 35 days. The emergence graph of _C. casuaria_ shows a sharp peak and has a lower emergence diversity than _P. scalaenum_ (1.71 versus 2.55), which emerges at a more equal rate throughout its emergence period.

One might hypothesize that if intraspecific competition was greater than interspecific competition, then abundant species should have both a longer emergence period and a more equal rate of emergence (i.e., higher emergence diversity) than less abundant species. Such a temporal separation of individuals within a species should reduce intraspecific competition. On the other hand, if interspecific competition is stronger than intraspecific competition, one would expect abundant species to have the same emergence diversity as less abundant species. My data indicated that there was no significant correlation between the abundance of a species and its emergence diversity, suggesting that interspecific competition is stronger than intraspecific competition.

An emergence period can consist of one or more phases. Emergence phases are periods of high emergence rates separated by periods when the emergence rate is low or there is no emergence. Generally each phase is due to the emergence of a different generation. The emergence pattern of 15 of the 32 species exhibited two phases, 10 species had only one phase and 6 species had three phases. Only one species, _Nanocladius_ sp. n. 1 (Fig.23c), showed no distinct phases. Instead, this species emerges in what Macan (1958) has termed "dribbles" throughout the emergence period. The mean number of phases for Tanypodinae, Orthocladiinae, Chironomini, and Tanytarsini was 1.7, 1.8 and 2.1, respectively. The mean number of phases per emergence period was 1.8 when all 32 species are considered.

Species with multi-phased emergence patterns can be further compared using the following three criteria: phase length, percentage of the emergence occurring in each phase, and time interval between phase modes (Tables XIII and XIV). The mean phase length of successive phases increases both in species with two- and with three-phased emergence patterns. A sign test showed that there was a significant increase ($p<5\%$) in the phase length of successive phases. Indeed, for all 58 phases (i.e., 10 species with one phase, 15 species with two phases, and 6 species with three phases), there was a significant correlation between the time of year and phase length ($r = 0.58$, $p<1\%$). The linear regression line is

$$\text{phase length (days)} = 1.2 \text{ (sample interval number)} + 12.0$$

For example, if a phase mode occurs during the 10th sampling interval, the expected phase length would be $1.2\ (10) + 12 = 24$ days.

For the 23 species for which males and females could be associated, the ratio of males to females was significantly less than one for 14 species and significantly higher than one for two species (Table XIII). The ratio of males to females among all 26,726 adults collected was 0.8. Generally the ratio of males to females declined steadily between the start and end of an emergence phase (Fig. 34).

C. Larval Phenology and Life Histories

With few exceptions chironomids pass through four

TABLE XIII Comparison of 15 species with a 2-phased emergence pattern. Phase length and interval between phase modes (T_{1-2}) are expressed in days. Species arranged in order of abundance.

	Phase Length		% Emergence		
Species	1st phase	2nd phase	1st phase	2nd phase	T_{1-2}
Tanytarsus dispar	34	75	23	77	40
Stempellina leptocelloides	41	66	39	61	54
Larsia pallens	21	28	22	78	24
Tanytarsus limneticus	32	45	33	67	40
Parakiefferiella sp.n.1	31	51	47	53	27
Stempellina sp.n.2	32	26	43	57	50
Heterotrissocladius changi	16	39	41	59	77
Cricotopus bicinctus	21	32	66	34	73
Stempellina sp.n.1	29	55	20	80	67
Polypedilum braseniae	25	28	45	55	40
Paracladopelma undine	35	34	65	35	26
Tanytarsus curticornis	29	31	69	31	36
Microtendipes pedellus	25	16	94	6	38
Psectrocladius simulans	31	34	23	77	23
Labrundinia pilosella	21	50	29	71	45
Means	28	41	44	56	44

TABLE XIV Comparison of six species having a 3-phased emergence pattern. The phase length and the interval between phase modes are expressed in days. The interval between the modes of the 1st and 2nd phases is designated T_{1-2}, and that between the modes of the 2nd and 3rd phases as T_{2-3}. Species arranged in order of abundance.

	Phase length			% Emergence			Mode interval	
	1st phase	2nd phase	3rd phase	1st phase	2nd phase	3rd phase	T_{1-2}	T_{2-3}
Rheotanytarsus distinctissima	25	30	41	7	13	80	40	26
Paralauterborniella nigrohalterale	27	25	28	60	22	18	27	20
Paramerina fragilis	18	20	71	12	13	75	21	36
Corynoneura lobata	24	34	48	27	18	55	51	39
Limnophyes folliculatus	38	38	46	58	24	18	38	43
Ablabesmyia mallochi	14	30	42	20	32	48	22	20
Means	24	30	46	31	20	49	33	31

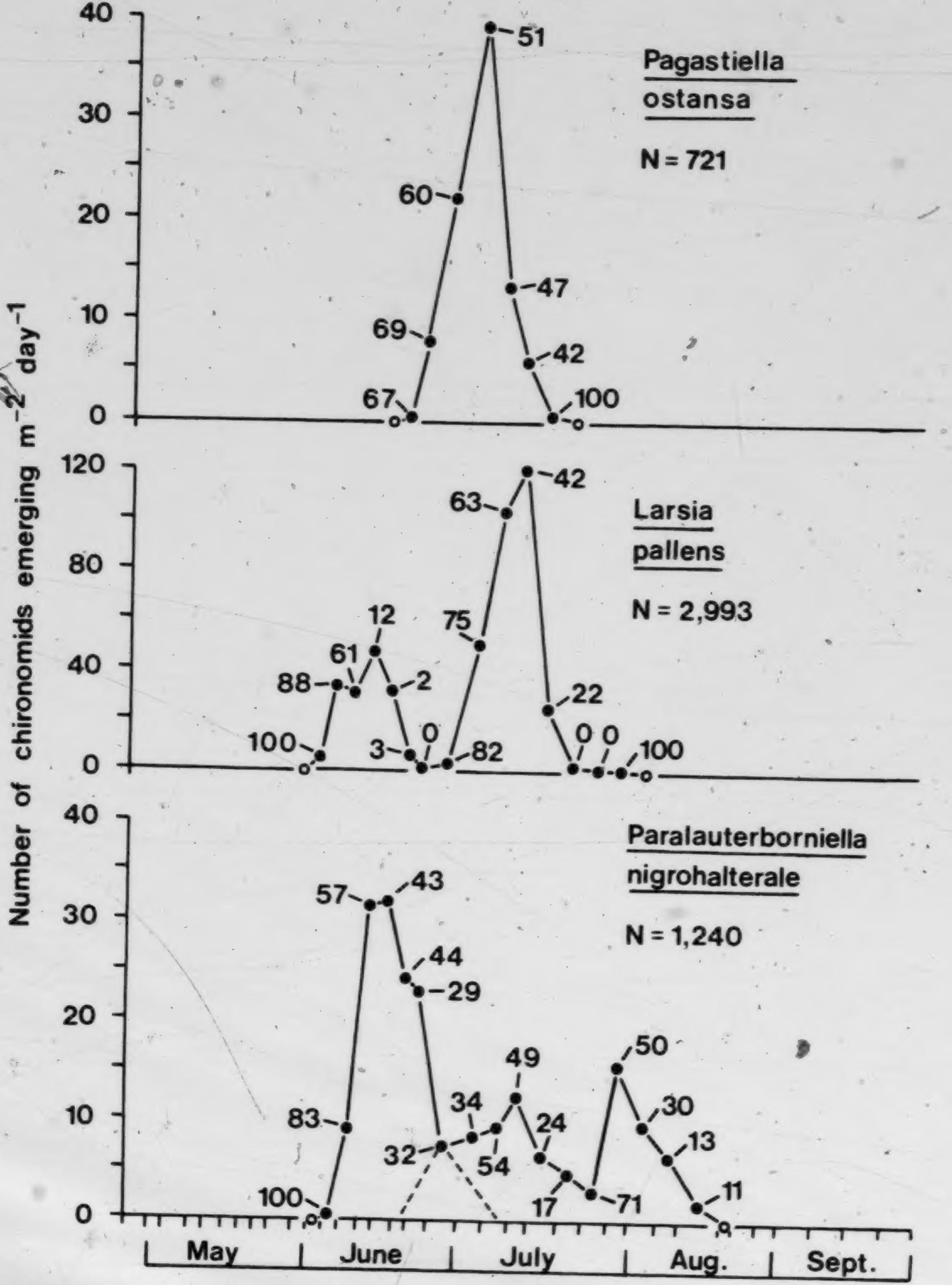

Fig. 34 Variation in percentage of males (numbers beside data points) throughout the emergence periods of three chironomid species.

larval instars (Ford 1959). Instars can be easily separated by measuring the length of the head capsule, with that of each successive instar being 1.5-1.7 times longer than that of the preceding one. All 8,025 larvae collected between November 1, 1971 and December 12, 1973 were mounted on slides, identified and measured. First instar larvae (larvules) were omitted from the analysis of larval phenology for the following reasons:

1) Only 73 Instar I larvae were collected. This represents only 0.9% of the total larvae. I am certain that this low number is not a result of the sampling technique used, since I utilized sieves with very fine mesh (80 μ) to sort the larvae from the sediment. The first instar generally lasts only a few days (Thienemann 1954), and this may explain the small number collected.

2) The small size and the weakly-chitinized head capsule made it difficult to mount the larvules on slides. Often the abdomen would wrap itself around the larvule's head, making identification impossible.

3) There are considerable morphological differences between Instar I larvae and the other larval instars (Thienemann 1954). Differences are especially pronounced in the appearance of the mentum and the antennae, two structures that are often used to identify larvae to species. Larvules would therefore have to be associated with the other larval instars through laboratory rearing, a time-consuming operation.

The 8,025 larvae collected between November 1, 1971 and December 12, 1973 were distributed among months as following: January (0), February (313), March (383), April (0), May (415), June (1,130), July (1,573), August (1,324), September (963), October (1,336), November (391), December (197). No samples were collected in January or April. Plant samples as well as sediment samples were collected in June, July, August and October (see page 49) and this accounts for the large number of larvae collected for these months. All 197 larvae collected for December came from the wire mesh cages containing Sparganium and willow leaves. Sediment samples were collected in all months except January, April and December. The variations in the number of larvae collected for each month therefore reflects variations in sampling effort as well as actual changes in population density.

The 32 most abundant species (those with yearly emergences of 50 males/m^2 or more - see Tables VIII-XI, pages 55 to 59) accounted for 7,182, or 89.5%, of the 8,025 larvae collected. Seasonal changes in percent abundance of larval instars II-IV of these 32 species are shown in Figures 35-41. The total number of larvae collected is shown in brackets after each species. The number of larvae collected for each month is given opposite the letter "N". The horizontal line or lines opposite the letter "A" indicate the times of emergence, and the vertical crossbars indicate the emergence peaks. More detailed information on emergence patterns has

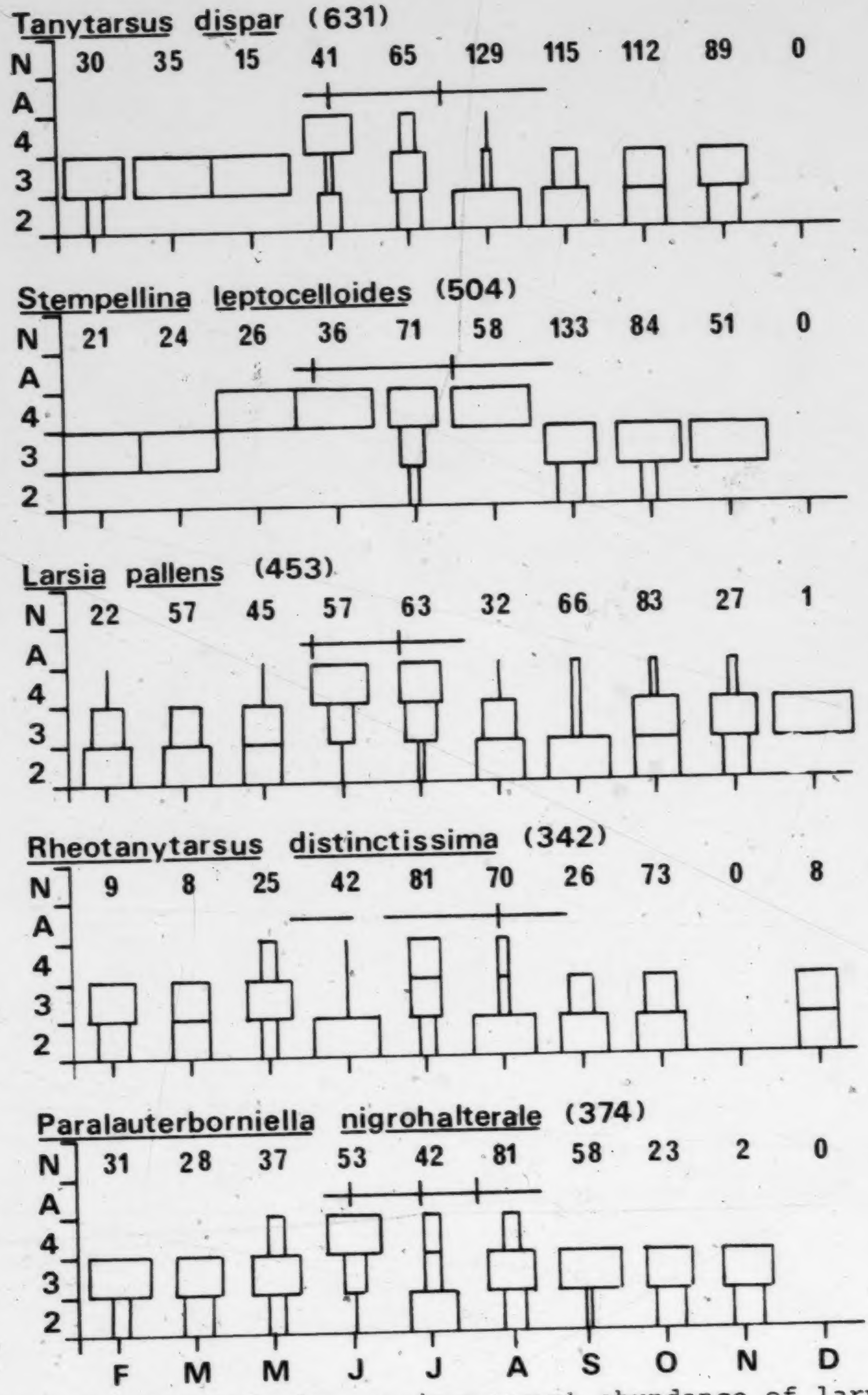

Fig. 35 Seasonal changes in percent abundance of larvae of five chironomid species. See text for explanation of Fig. 35 - 41. Species arranged in order of decreasing abundance as determined from emergence data.

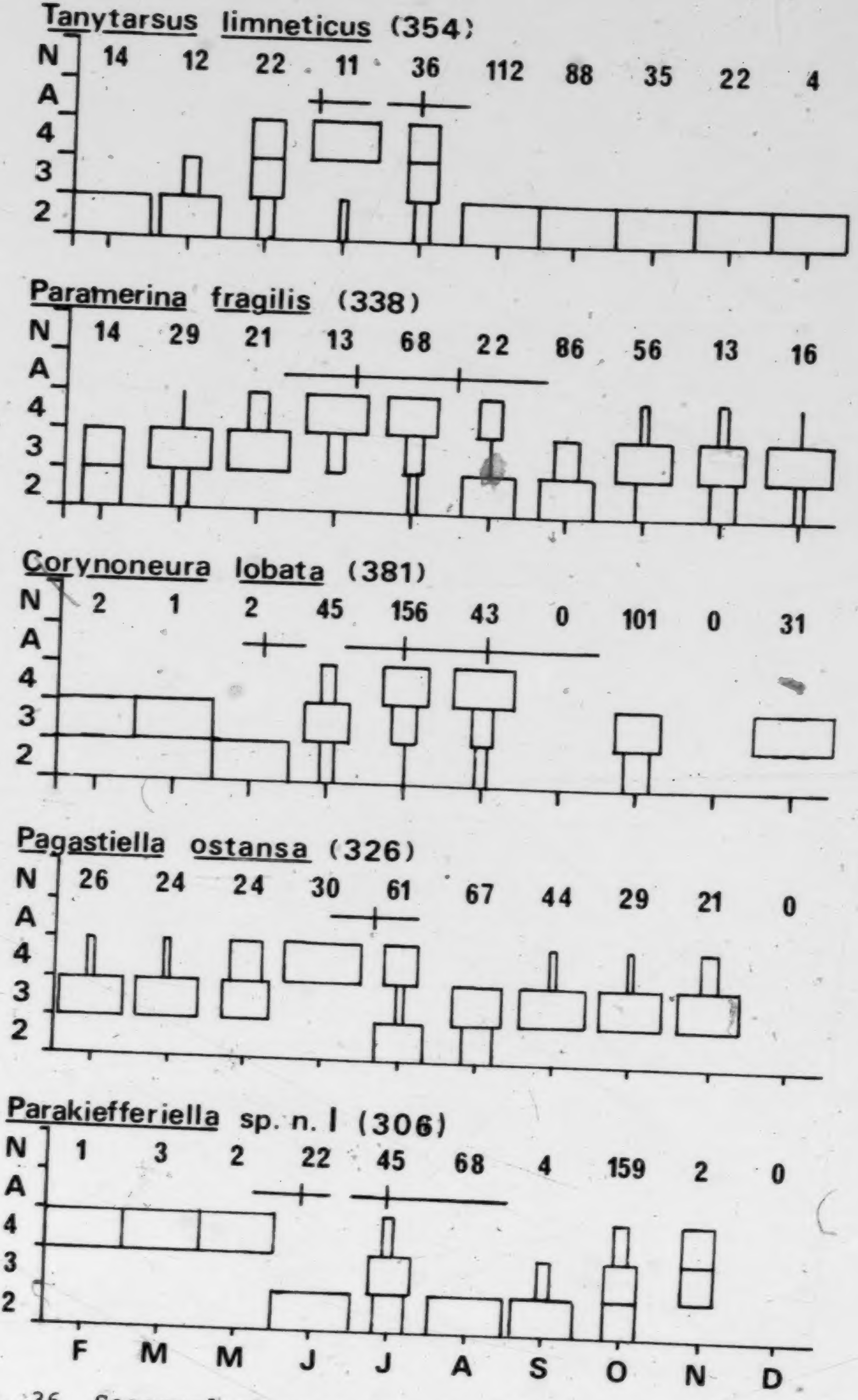

Fig. 36 Seasonal changes in percent abundance of larvae of five chironomid species.

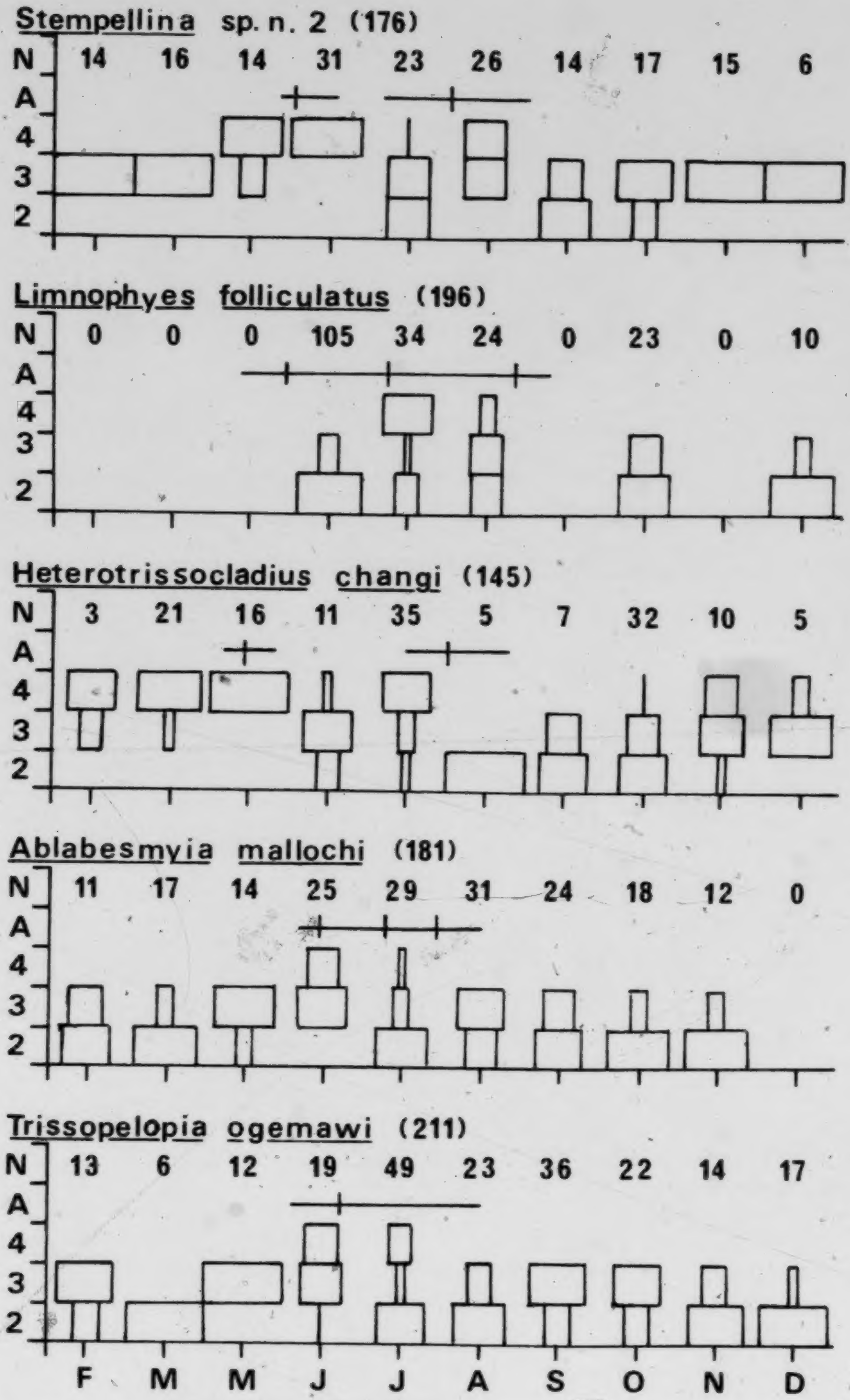

Fig. 37 Seasonal changes in percent abundance of larvae of five chironomid species.

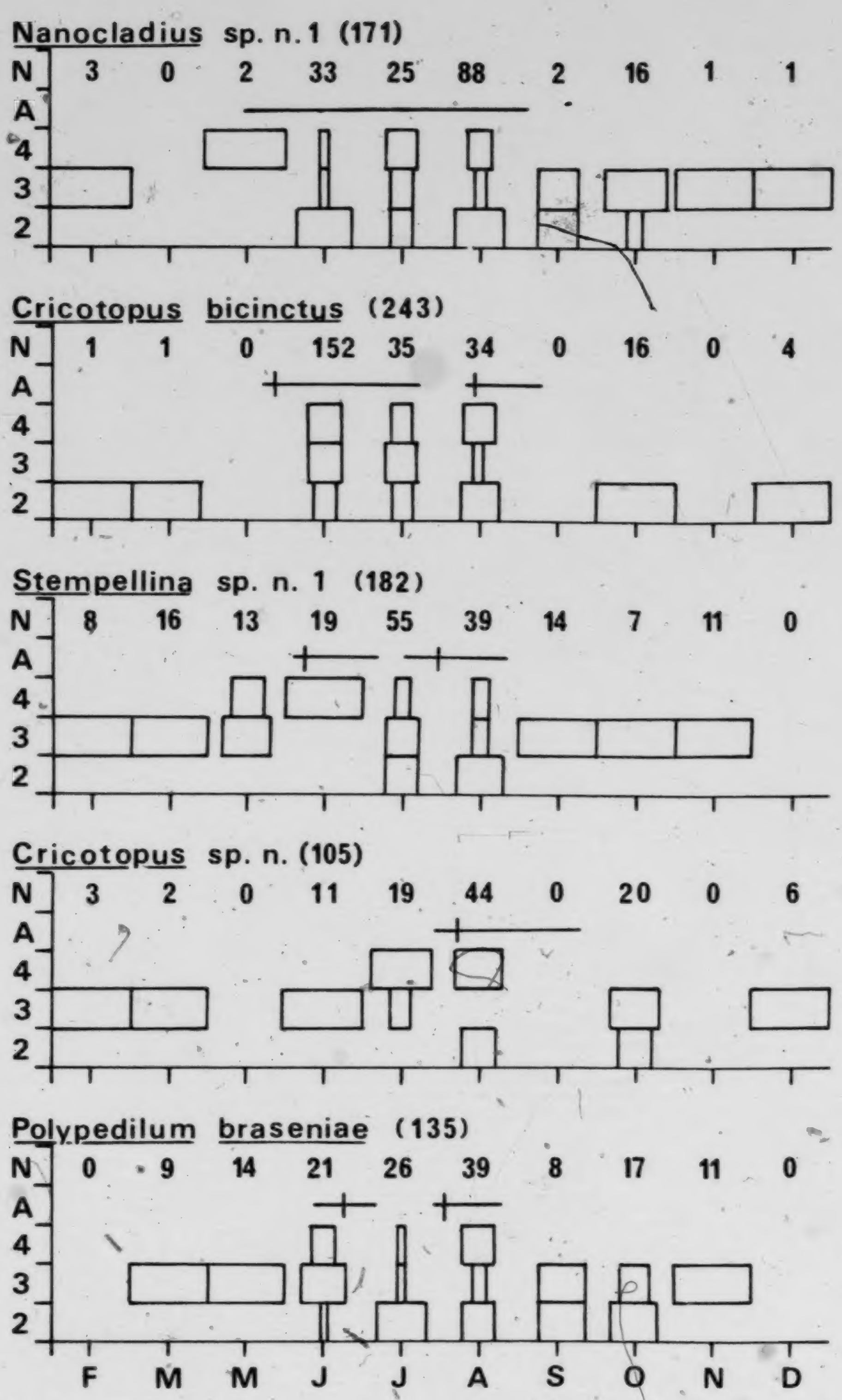

Fig. 38 Seasonal changes in percent abundance of larvae of five chironomid species.

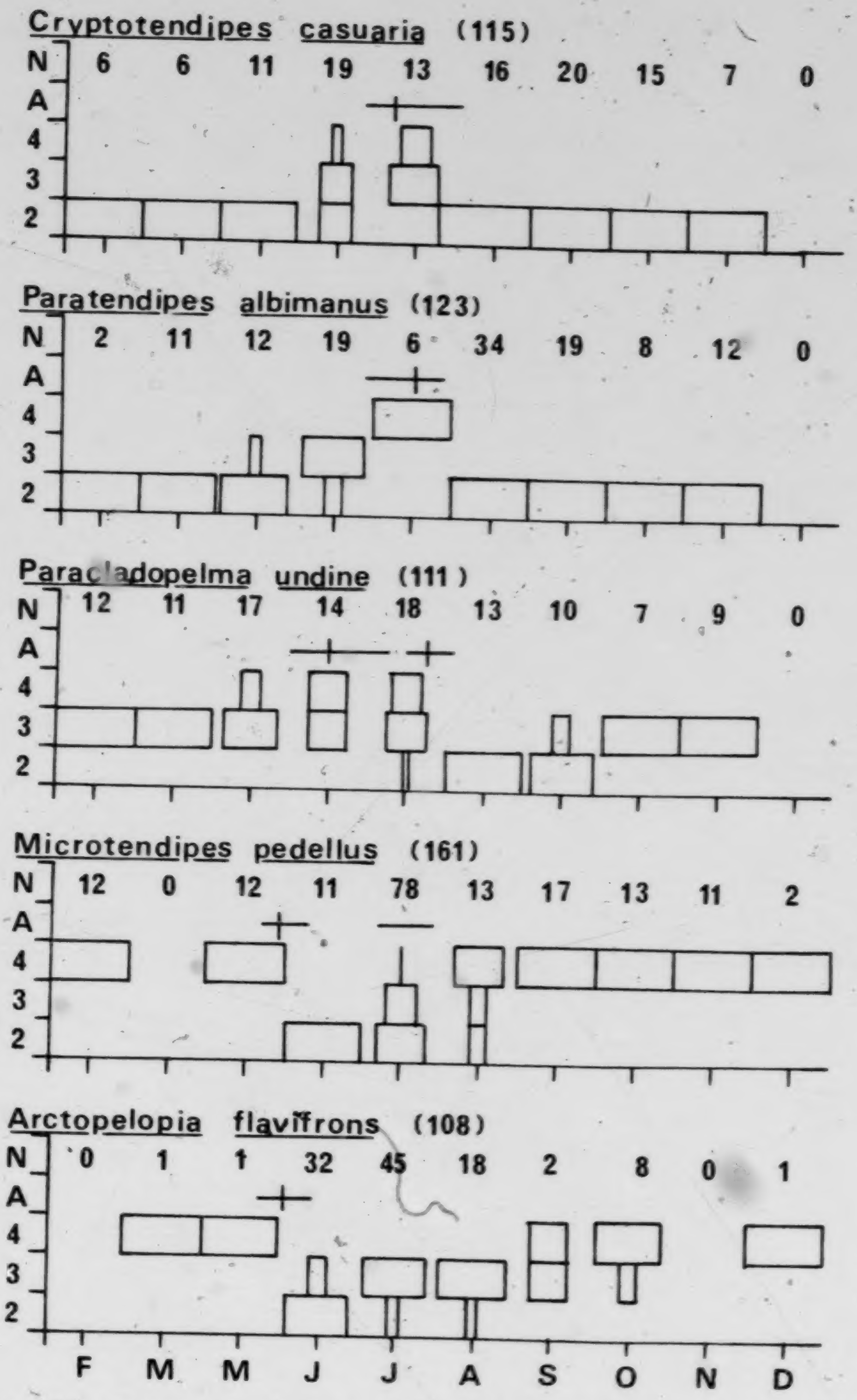

Fig. 39 Seasonal changes in percent abundance of larvae of five chironomid species.

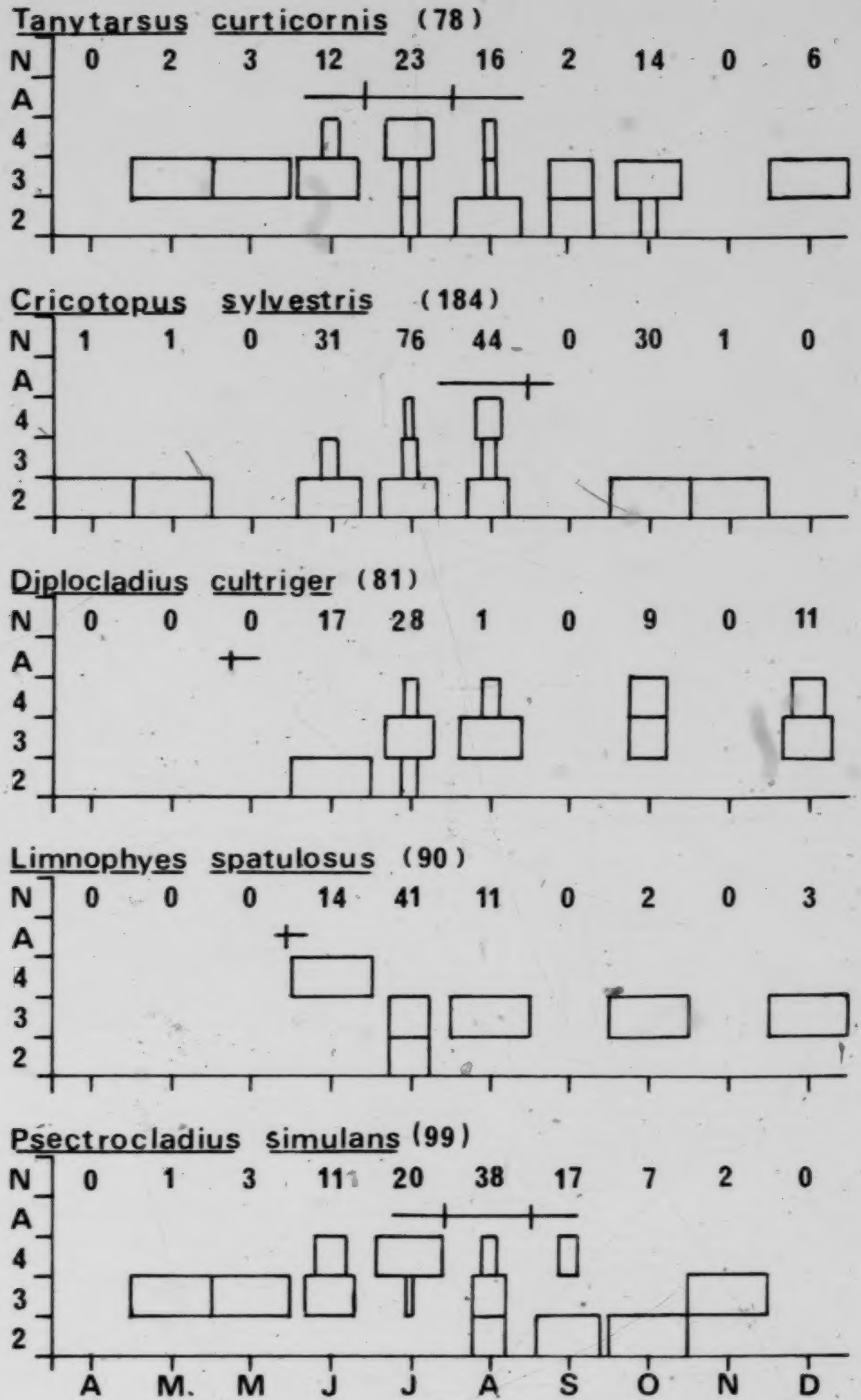

Fig. 40 Seasonal changes in percent abundance of larvae of five chironomid species.

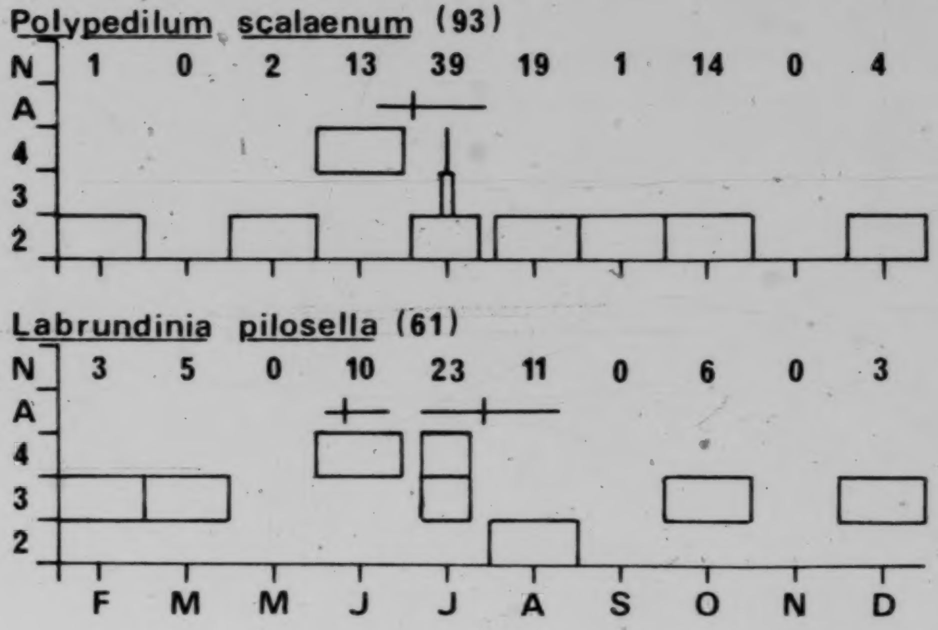

Fig. 41 Seasonal changes in percent abundance of larvae of two chironomid species.

already been presented and the lines are included only to facilitate correlation of seasonal changes in abundance of larval instars with times of emergence. Width of the bars opposite the numbers 2, 3 and 4 indicates the percent abundance of second, third and fourth instar larvae, respectively. The width of the bars above each month totals 100%. January and April have been omitted from the abscissa since no samples were collected during those months.

Actual total number of larvae collected of each species varied from 61 for Labrundinia pilosella to 631 for Tanytarsus dispar. Based on emergence data, L. pilosella was also the least abundant and T. dispar the most abundant. However, for many other species, the abundance rank based on larval data differed from that based on emergence data. For example, Cricotopus trifasciatus was the 27th most abundant species according to emergence data but the 16th most abundant based on larval data. These discrepancies are, however, understandable, since the larval samples were not collected in proportion to the abundance of the different microhabitats present in the stream. Such a sampling design, stratified proportional to the abundance of the different microhabitats, would have been extremely difficult to set up. The emergence data is not susceptible to such sampling difficulties and therefore gives a much more accurate indication of the relative abundance of the different species.

For most species, seasonal changes in abundance of larval instars could be related with emergence periods, therefore giving a good indication of the life history of the species. These are summarized below:

Tanytarsus dispar. Both the larval and emergence data indicate that *T. dispar* is the most abundant species in the Bigoray River. Large numbers of this pale green species were frequently seen swarming near willow bushes by the river. Larvae overwinter in the second and third instar, with the number of third instar larvae increasing throughout the winter. However, no Instar IV larvae were collected between September and May. Both emergence and larval data indicate two generations per year, with the summer generation lasting two months (mid-June to mid-August).

Stempellina leptocelloides. These small, dark-brown Tanytarsini are the second most abundant species in the stream. It also has two generations per year and emerges about the same time as *T. dispar*. *Stempellina leptocelloides* larvae overwinter in the third instar. Also, fourth instar larvae and the first emergence occur somewhat earlier in *S. leptocelloides* than in *T. dispar*. These differences are likely related to the smaller size of *S. leptocelloides*.

Larsia pallens. These small, pale Tanypodinae have two generations per year. The 4-week summer generation (early June to early July) passed so quickly that it is not very clearly depicted in the larval data. Although fourth instar larvae are present throughout the year, most larvae overwinter in the second and third instars. The predaceous larvae do not seem to grow during the winter. The above three species accounted for 41% of the adult male chironomids which emerged from stream in 1973.

Rheotanytarsus distinctissima. Larval and emergence data clearly indicate that this species undergoes at least two generations per year and possibly even three (Fig. 26B, p.69). Larvae overwinter in the second and third instars and do not seem to grow during winter.

Paralauterborniella nigrohalterale. Larval data would indicate that this species passes through at least two generations a year, and analysis of changes in sex ratios during the emergence period provide good evidence that there are three generations per year (Fig. 34, p.84). The first summer generation lasts 4 weeks (mid-June to mid-July) and the second summer generation lasts 3 weeks (mid-July to early August). Overwintering occurs in the second and third larval instars.

Tanytarsus limneticus. Larval and emergence data clearly indicate two generations per year with the summer generation lasting 6 weeks (late May to mid-July). This species differs from *T. dispar* by overwintering exclusively in the second instar instead of in both second and third instars.

Paramerina fragilis. Larval data indicate two generations per year. The emergence peak on the 17th sampling interval (Fig. 27D, p.70) may be a sampling error, since it is based on only a single datum point. Like *Larsia pallens*, this is a predaceous species and can overwinter in the 2nd, 3rd or 4th instars, but primarily in the third instar.

Corynoneura lobata. This is the smallest species in the stream (larval length 1.8-2.3 mm). It passes through three generations per year, with the first and second summer generation lasting 8 and 6 weeks, respectively. Overwintering occurs as third instar larvae.

Pagastiella ostansa. Both larval and emergence data show this species to have only one generation per year, with most larvae overwintering in the third instar, but some also in the fourth instar.

Parakiefferiella sp. n. 1. Larval and emergence data clearly indicate two generations per year, with all larvae overwintering in the fourth instar.

Stempellina sp. n. 2. The life cycle of this species is almost identical to that of *S. leptocelloides*, with two generations per year and overwintering in the third larval instar. Emergence periods of the two species are also synchronous.

Limnophyes folliculatus. Emergence data indicate three generations per year, but there is little larval data for the overwintering generation. Overwintering seems to occur in the second and third larval instars.

Heterotrissocladius changi. Larval and emergence data clearly indicate two generations per year, with a long summer generation lasting from mid-May to late July. Overwintering occurs in the third and fourth larval instars, with some growth during winter months.

Ablabesmyia mallochi. Larval data suggest at least two generations and emergence data indicate three generations, with the two summer generations lasting three weeks each. Larvae do not seem to grow during winter, which is spent in the second and third instars.

Trissopelopia ogemawi. Larval and emergence data suggest that this large predator goes through only a single generation per year with no growth during winter, which is spent in the second and third larval instars.

Nanocladius sp. n. 1. This species emerges in "dribbles" throughout the summer with no clear emergence peaks. Larval data indicate at least two generations per year. The small size (larval length: 2.5-3.1 mm) of this Orthocladiinae would suggest three generations, with considerable overlap between generations. Overwintering seems to occur exclusively in the third instar.

Cricotopus bicinctus. Larval data indicate two generations per year with larvae overwintering in the second instar. Emergence data indicate that a small proportion of the population may go through an extra summer generation.

Stempellina sp. n. 1. As for the other two Stempellina species, this species has two generations per year and overwinters in the third larval instar. It emerges a week before the other two species; hence the designation of species 1. It is, however, less abundant than the other two species.

Cricotopus sp. n. 1. This species passes through only a single generation a year, with an emergence period that is synchronous with the second emergence period of *C. bicinctus*. *Cricotopus* sp. n. 1 overwinters in the third larval instar instead of the second instar (re. *C. bicinctus*).

Polypedilum braseniae. Larval and emergence data clearly indicate two generations per year, with the summer generation lasting 6 weeks (mid-June to early August). Larvae do not seem to grow during winter months, which are spent in the third larval instar.

Cryptotendipes casuaria. This species passes through only a single generation per year and the larvae overwinter in the second instar.

Paratendipes albimanus. The life cycle of this species is similar to *C. casuaria*, with one generation per year and overwintering in the second instar. The emergence periods, however, are not synchronous; *C. casuaria* emerging mainly between July 1 and 15 and *P. albimanus* emerging between July 15 and 26.

Paracladopelma undine. Larval and emergence data indicate two generations per year with overwintering occurring in the third larval instar.

Arctopelopia flavifrons. This species has only a single generation per year and an early emergence period (May 18-June 7). Larvae overwinter in the fourth instar.

Tanytarsus curticornis. This species passes through two generations per year as did T. dispar and T. limneticus. However, the three species show differences in overwintering stages, with T. limneticus overwintering only in the second instar, T. dispar overwintering in the second and third instars, and T. curticornis overwintering only in the third instar. The emergence periods of T. dispar and T. curticornis are synchronous. Each of the two emergence periods of T. limneticus precedes the emergence periods of the other two Tanytarsus species by two weeks.

Microtendipes pedellus. Most of the population passes through only a single generation per year with an early emergence period (May 21-June4). Some of the larvae of the new generation reach the fourth instar by August and emerge at that time. Most of the population, however, overwinters in the fourth larval instar.

Cricotopus sylvestris. Like Cricotopus sp. n. 1, this species passes through only a single generation per year, with the emergence peak occurring later than that of any other species in the stream. The larvae overwinter in the second instar, as do those of C. bicinctus.

Diplocladius cultriger. This is the first species to emerge in the stream. It passes through only a single generation per year and appears to overwinter in the third and fourth larval instars. Larval data are, however, only available for 5 months.

Limnophyes spatulosus. This species passes through only a single generation per year and not three, as in L. folliculatus. The emergence period is synchronous with the first emergence period of L. folliculatus. Larvae appear to overwinter in the third instar, but larval data are scanty for the winter months.

Psectrocladius simulans. Larval data clearly indicate the presence of two generations per year. However, emergence of the winter generation is small compared to emergence of the summer generation. Overwintering appears to occur in the third larval instar.

Polypedilum scalaenum. Larval and emergence data both indicate one generation per year, with larvae overwintering in the second instar. This life cycle differs considerably from that of P. braseniae, which passes through two generations per year and overwinters in the third larval instar. The single emergence period of P. scalaenum occurs primarily between the two emergence periods of P. braseniae.

Labrundinia pilosella. This species goes through two generations per year and overwinters in the third larval instar.

In summary, of the 32 species analyzed, 11 species (34%) were univoltine, 15 species (47%) were bivoltine, and 6 species (19%) were trivoltine. The pattern of voltinism in the four taxonomic groups was as follows:

		Univoltine	Bivoltine	Trivoltine
Tanypodinae	(6 species)	33%	50%	17%
Orthocladiinae	(11 species)	36%	36%	28%
Chironomini	(8 species)	63%	25%	12%
Tanytarsini	(7 species)	0%	86%	14%

Particularly noticeable is the high percentage of univoltine species among Chironomini, and the complete lack of univoltine species among Tanytarsini.

All the above species overwintered as larvae; indeed, overwintering in any other life stage (egg, pupa or adult) is unknown among aquatic Chironomidae (Thieneman 1954, Oliver 1971). The percentage of species that overwinter in various larval instars was as follows: second instar only (19%), second and third instars (16%), third instar only (44%), third and fourth instars (12%), and fourth instar only (9%). Therefore, the most common overwintering stage in Bigoray River chironomids is the third larval instar.

D. Seasonal Changes in Larval Densities

The mean density of all larvae inhabiting the bottom sediment varied from $3.1 \times 10^3/m^2$ on June 20, 1971 to $52.9 \times 10^3/m^2$ on October 1, 1973 (Fig. 42). The mean density for the entire 23-month period (Nov. 1, 1971-Oct. 1, 1973) was 19.9×10^3 larvae/m^2 (95% C.L.: 11.7-21.6). Minimum density occurred in June in both 1972 and 1973, and maximum density was reached in March. Confidence limits indicated that the decline in density in October and November, 1972, were not significant (P > 5%). However, a similar decline, this time significant (P < 5%) occurred in August, 1973, and may have resulted from the high rate of emergence at the start of that month (see Fig. 21, p.63). Larvae were more abundant during May-September, 1973 than during the same time in 1972. Mean monthly water temperature during May-September, 1973 averaged 1.1 Centigrade degrees higher than during the corresponding period in 1972. Although 67 mm more rain fell during May-September, 1973 than during the same period in 1972, rainfall in 1973 was more equally distributed and there were fewer spates than in 1972.

When the Tanypodinae, Orthocladiinae and Chironomini are considered separately (Fig. 43) the pattern of seasonal changes becomes more variable; however, in all cases the minimum density occurs in June. In the Tanytarsini, minimum density occurs in November and December as well as in June. Confidence limits could not be calculated for the four major taxonomic groups because the larvae collected from the 12 sediment samples taken on each date were pooled prior to selecting the random subsamples of larvae that were mounted on slides and identified. Over the 23-month sampling period, the mean density of larvae occurring in the sediment was as follows for the four major taxonomic groups:

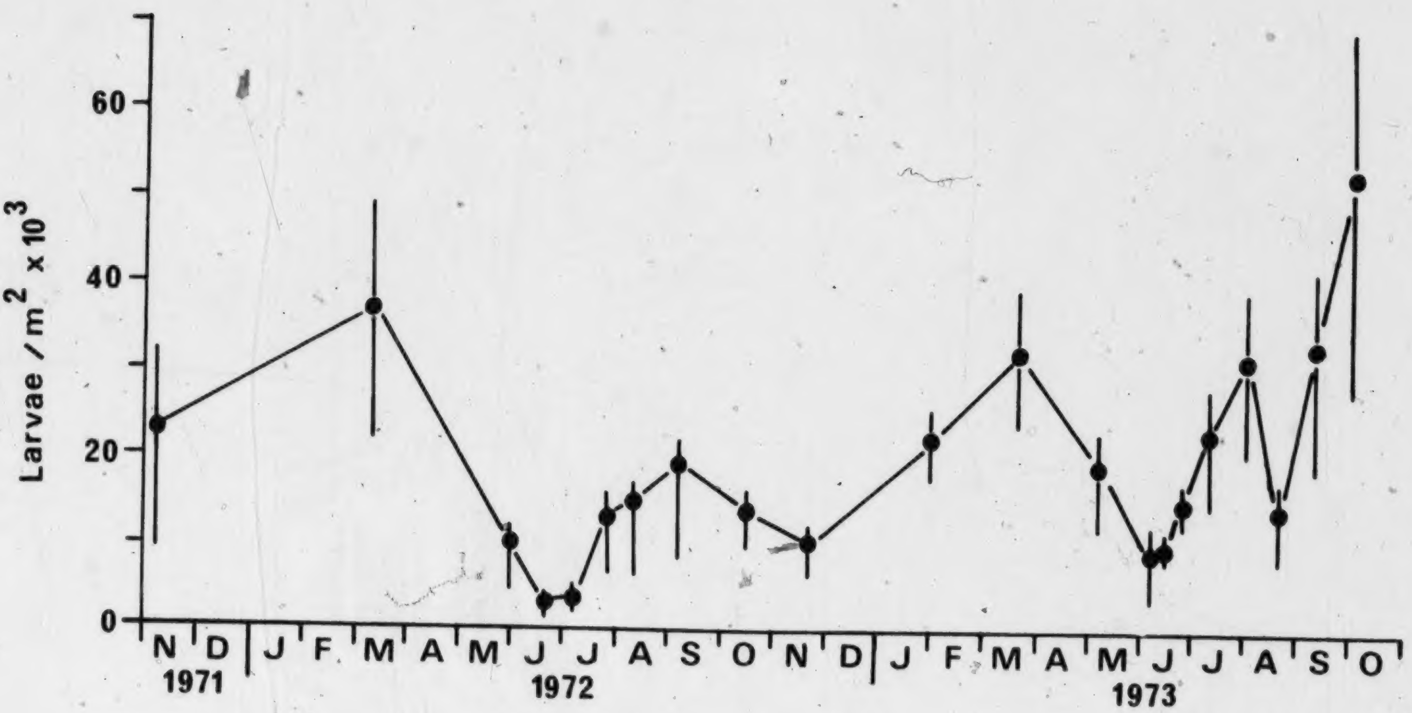

Fig. 42. Mean density of bottom-inhabiting chironomid larvae in the Bigoray River. Vertical lines are 95% confidence limits.

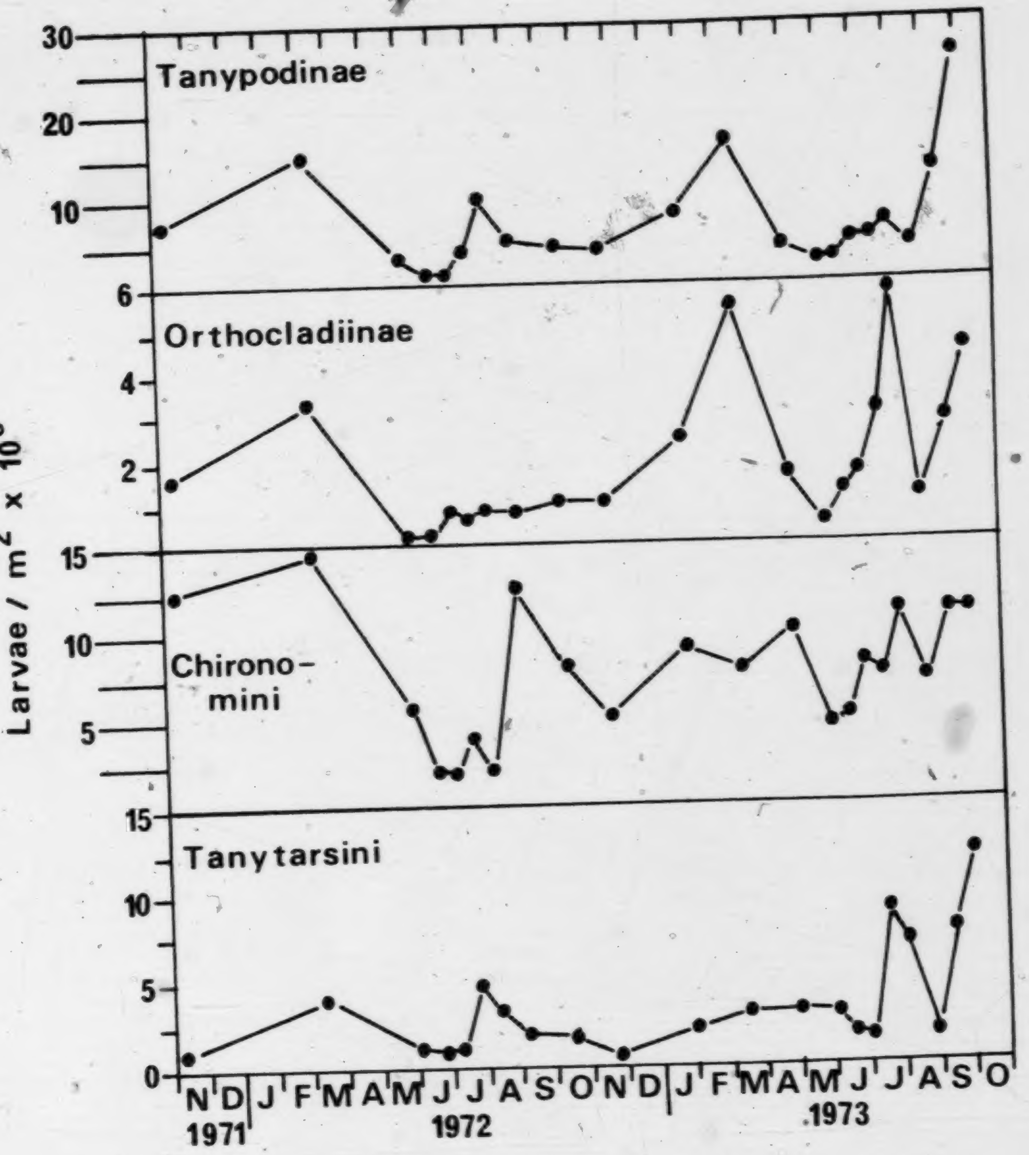

Fig. 43 Seasonal changes in mean density of Tanypodinae, Orthocladiinae, Chironomini and Tanytarsini larvae in Bigoray River sediment.

	Mean density (larvae/m^2 x 10^2)	95% Confidence Limits
Tanypodinae	6.8	3.1 - 7.1
Orthocladiinae	1.9	1.1 - 2.1
Chironomini	7.5	4.8 - 8.4
Tanytarsini	3.3	1.6 - 3.5

The abundance of larvae on the various aquatic plants, submerged wood, leaves and sponges was measured on six dates in 1973 (Table XV). Densities could be expressed as: 1) numbers per unit weight of substrate, or 2) numbers per unit volume of substrate, or 3) numbers per unit surface area of substrate. For clumps of filamentous algae and sponge colonies, the appropriate unit would be numbers/volume since the larvae occur within the algal clumps and sponge colonies, as well as along their outer surfaces. For _Sparganium_, _Potamogeton_, _Hippuris_, moss, wood and leaves, the larval density is best expressed in numbers/surface area, since the larvae are found only on the surface of these substrates. This unit is, however, seldom used since it is difficult to calculate the surface area of irregular-shaped aquatic vegetation. Also, some of the larvae, such as _Glyptotendipes_ and _Stenochironomus_, will burrow into aquatic vegetation and submerged wood. As the vegetation decays and becomes softer, many species that do not normally burrow will also be found inside the vegetation. This was especially noticeable in decaying _Sparganium_, whose sponge-like cortex contained many

TABLE XV Abundance of chironomid larvae in various microhabitats. Units are number of larvae/gm dry weight of substrate except wood, for which the units are number of larvae/cm^2 of wood.

Date 1973	Number of samples	Mean density	95% confidence limits
A. *Sparganium*			
June 11	3	21	5 - 81
June 21	5	52	26 - 102
July 11	3	60	15 - 243
July 31	3	62	37 - 103
Aug. 20	3	22	14 - 35
Oct. 1	3	373	114 - 1,216
All dates	20	93	62 - 155
B. *Potamogeton*			
June 11	3	124	64 - 239
June 21	5	140	86 - 228
July 11	3	379	160 - 898
July 31	4	101	53 - 193
Aug. 20	4	53	26 - 107
Oct. 1	4	278	158 - 489
All dates	23	171	124 - 236
C. *Hippuris*			
June 11	3	229	111 - 474
June 21	3	457	212 - 987
July 11	3	655	291 - 1,474
July 31	5	175	113 - 271
Aug. 20	3	257	120 - 550
Oct. 1	4	984	448 - 2,027
All dates	21	466	335 - 648

- continued

Table XV (cont'd)

Date 1973	Number of samples	Mean density	95% confidence limits
D. Moss			
June 11	3	1,327	809 - 2,176
June 21	3	268	113 - 638
July 11	3	1,103	587 - 2,074
July 31	3	377	307 - 464
Oct. 1	3	1,817	520 - 6,341
All dates	15	978	631 - 1,516
E. Sponge			
July 11	3	80	25 - 251
July 31	3	5	1 - 23
Aug. 20	3	13	5 - 33
All dates	9	32	12 - 85
F. Filamentous algae			
June 11	3	535	79 - 3,643
July 11	3	637	408 - 994
July 31	3	376	109 - 1,293
Aug. 20	3	30	12 - 75
Oct. 1	3	352	317 - 391
All dates	15	351	186 - 663
G. Wood			
June 21	3	0.1	0.1 - 0.2
July 11	3	0.2	0.1 - 0.6
July 31	3	1.9	1.1 - 3.2
Aug. 20	3	0.5	0.1 - 1.9
Oct. 1	4	1.6	0.7 - 3.9
All dates	16	0.9	0.7 - 1.1

larvae. For all of the above cases, the appropriate unit would be number/unit volume of substrate. Since there was no unit of density that was suitable for all types of substrate examined, I expressed larval abundance for all substrate except wood in terms of number/gm dry weight of substrate, since this could be measured with greatest precision. Larval abundance on wood was expressed in terms of the wood's surface area.

Changes in larval abundance between June 11 and October 1, 1973 were similar on all plants except on moss. Larvae generally increased in abundance between June 11 and July 11, then decreased until August 20, and had increased again by October 1. Similar changes in abundance were observed in the sediment during this time (Fig.42, p.104).

Larvae were most abundant on moss, less abundant on Hippuris and Potamogeton, and least abundant on Sparganium. These differences are most likely the result of the greater surface area per unit dry weight of moss and Hippuris when compared to Potamogeton and Sparganium.

By December 21, 1973 the abundance of larvae inside the small wire-mesh cages filled with Sparganium (p.22) had reached 1.5 x 10^3 larvae/gm dry weight of Sparganium and still appeared to be increasing (Fig.44). However, the abundance of larvae inside the cages would probably not have increased much more, since the density of larvae on Sparganium growing naturally had been 1.8 x 10^3/gm dry weight on October

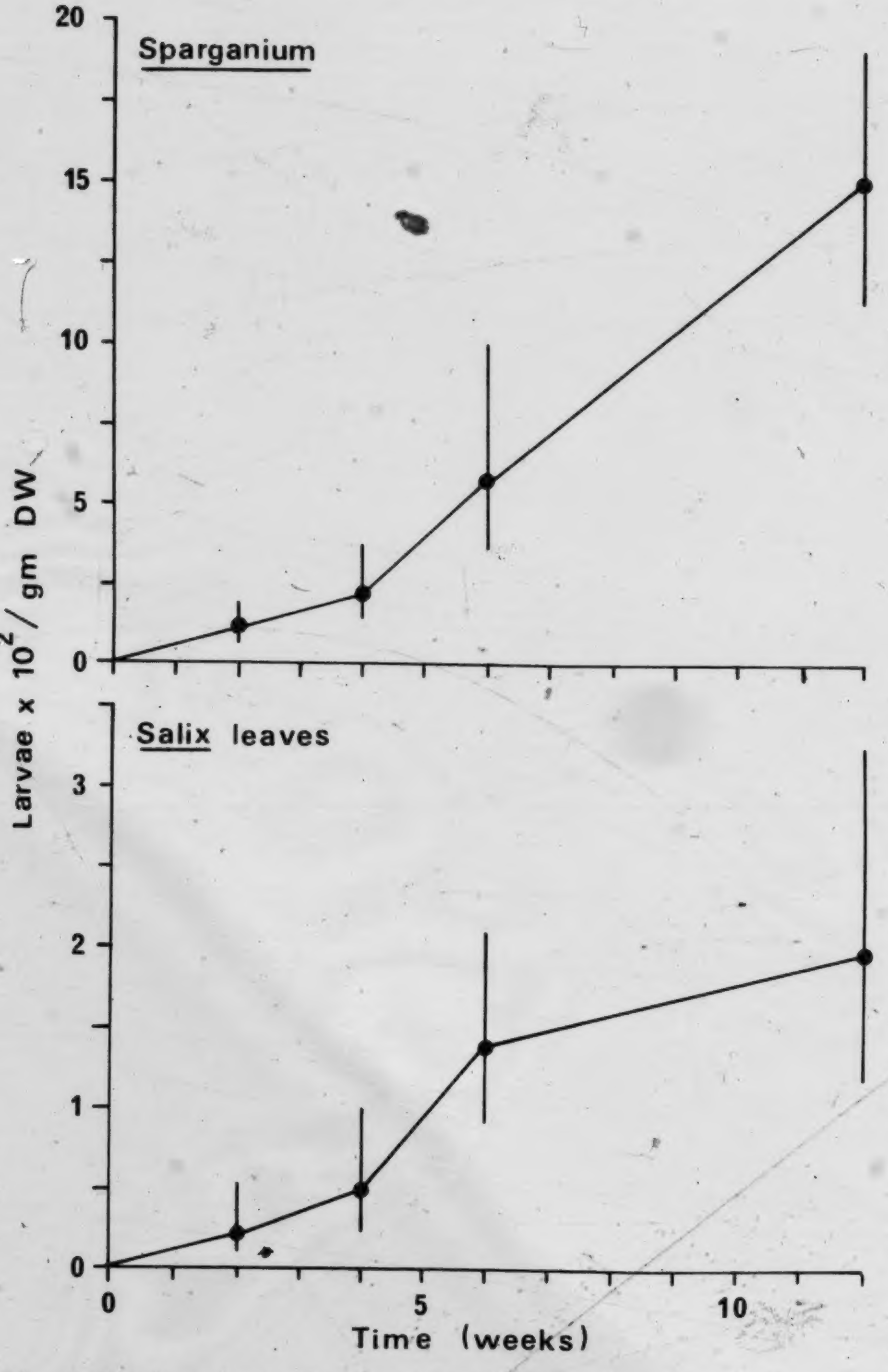

Fig. 44 Colonization of submerged Salix leaves and Sparganium by chironomid larvae. Plants placed in Bigoray River on September 24, 1973. Means and 95% confidence limits based on three samples.

9. It is likely, therefore, that the colonization curve would have levelled off between 1.5 and 1.8 x 10^3 larvae/gm dry weight. The abundance of larvae in the cages filled with Salix leaves seemed to be levelling off at 0.2 x 10^3 larvae/gm dry weight after 12 weeks.

On December 21, larvae were eight times more abundant on Sparganium than on Salix leaves. This was probably related to the faster rate of decomposition of Sparganium.

No sampler will provide estimates of larval densities in a habitat as structurally complex as the Bigoray River, with its submerged vegetation, sunken trees, bushes and sediment ranging from flocculant silt to hard-packed clay. Larval density underneath a unit area of stream surface can, however, be estimated by the 3-step procedure outlined below:

1) Estimate the abundance of the various microhabitats using the quadrat technique described on page 10. Results of these quadrat samples were given in Tables I-III (p.16-19), and are repeated in condensed form in the A columns of Table XVI.

2) Estimate the density of larvae per unit of microhabitat using the sampler best suited to each microhabitat. Larval densities on various plant types were presented in Table XV (p.107), and are repeated in condensed form in the B columns of Table XVI.

3) Multiply values obtained in step 1 by the values obtained in step 2, and then sum the products to obtain the

TABLE XVI Calculation of larval abundance per square meter of stream surface. Column A gives abundance of plant types in gm DW/m^2 except wood which is expressed in m^2 surface area/m^2. Column B gives abundance of larvae in numbers/gm DW except wood, for which the units are numbers/m^2. Column C = Column A x Column B, with the numbers rounded off to the nearest 100.

Plant type	July 5 - 11			July 31 - Aug. 3			Aug. 20 - 29		
	A	B	C	A	B	C	A	B	C
Sparganium	30.8	60	1,800	74.1	62	4,600	70.6	22	1,600
Potamogeton	13.7	379	5,200	22.5	101	2,300	31.0	53	1,600
Hippuris	2.6	655	1,700	2.1	175	400	2.7	275	700
Fil. algae	0.1	637	100	0.4	376	200	10.2	30	300
Wood	0.6	2,000	1,200	0.7	19,000	13,300	0.5	5,000	2,500
Total plant-inhabiting larvae/m^2			10,000			20,800			6,700
Sediment-inhabiting larvae/m^2			23,400			31,400			13,800
Total larvae/m^2			33,400			52,200			20,500

mean total density of larvae. These multiplications and summations are given in the C columns of Table XVI.

These calculations could, of course, only be made for the three dates on which macrophyte abundance was determined with the quadrat technique. Since quadrat samples could not be collected on the same dates as the larval samples, quadrat data collected July 5, August 3, and August 29 were combined with larval data collected July 11, July 31 and August 20, respectively.

Above calculations indicated that total larval densities per square meter of stream varied between 20,500 and 52,200 during July and August, 1973. Larvae on plant material accounted for 30-40% of the total larvae. Although larvae were abundant on moss, this microhabitat was insignificant when compared with others and has not been included in Table XVI. The sponge microhabitat is similarly insignificant compared to others.

E. Microhabitat Distribution of Larvae

The distribution of all 8,025 collected larvae among nine microhabitats is shown in column A of Table XVII. If the four major taxonomic groups were randomly distributed among the different microhabitats, then the percentages in columns B - E should have been similar to the percentages in column A. Based on chi-squared tests, the percentages in columns B - E were significantly different ($P < 1\%$) from those

TABLE XVII A comparison of the percentage of chironomid larvae collected from nine microhabitats in the Bigoray River. The "+" sign indicates less than 1% occurrence.

Microhabitat	(A) All larvae	(B) Tanypodinae only	(C) Orthocladiinae only	(D) Chironomini only	(E) Tanytarsini only
Sediment	29	41	6	68	33
Sparganium	12	5	20	4	6
Potamogeton	10	8	11	4	17
Hippuris	12	13	14	4	15
Moss	12	10	17	3	12
Fil. algae	6	3	11	1	2
Sponge	4	3	4	6	3
Wood	12	13	13	10	11
Leaves	3	4	4	+	1
	100%	100%	100%	100%	100%

in column A. The Tanypodinae were more abundant on sediment (41% compared to the expected value of 29%), and disproportionately scarce on *Sparganium* (5% versus the expected value of 12%). The Chironomini were also more abundant on the sediment than expected by chance alone (68% versus 29%). In contrast, Orthocladiinae appeared to avoid sediment, (6% versus 29%) and frequent *Sparganium* and to a lesser extent moss and filamentous algae. The Tanytarsini showed a tendency to avoid *Sparganium* and instead select *Potamogeton*.

The percentage distribution of larvae among the nine microhabitats was also calculated for each of the 32 most abundant species (Table XVIII). The 20 species that occurred either exclusively or predominantly in only one microhabitat are listed below. Following each species is the percentage of larvae found in the particular microhabitat.

1) *Sediment*:

Cryptotendipes casuaria (100%), *Paratendipes albimanus* (100%, *Paracladopelma undine* (99%), *Pagastiella ostensa* (99%), *Paralauterborniella nigrohalterale* (98%), *Polypedilum braseniae* (96%), *Stempellina* sp. n. 2 (91%), *Tanytarsus limneticus* (91%), *Stempellina* sp. n. 1 (89%), *Larsia pallens* (86%), *Stempellina leptocelloides* (85%), *Ablabesmyia mallochi* (63%), *Heterotrissocladius changi* (60%).

2) *Sparganium*:

Cricotopus trifasciatus (73%), *Diplocladius cultriger* (63%).

TABLE XVIII Percent abundance of the 32 most abundant chironomid species in nine microhabitats in the Bigoray River. Calculations of χ^2 values (in brackets) explained in text. Species arranged in order of decreasing abundance.

Species	Sediment	Sparganium	Potamogeton	Hippuris	Moss	Algae	Sponge	Wood	Leaves
Tanytarsus dispar (27)	36	2	11	13	11	1	3	23	0
Stempellina leptocelloides (157)	85	2	6	0	0	2	5	0	0
Larsia pallens (160)	86	0	4	4	0	0	2	3	1
Rheotanytarsus distinctissima (109)	6	11	35	26	14	1	2	4	1
Paralauterborniella nigrohalterale (231)	98	1	0	0	1	0	0	0	0
Tanytarsus limneticus (189)	91	1	1	1	0	1	1	1	3
Paramerina fragilis (13)	34	12	6	21	8	2	0	11	6
Corynoneura lobata (106)	1	29	21	14	5	1	1	7	21
Pagastiella ostensa (238)	99	0	0	0	0	0	1	0	0
Parakiefferiella sp.n.1 (118)	3	4	8	18	6	3	16	39	3
Stempellina sp.n.2 (192)	91	9	0	0	0	0	0	0	0
Limnophyes folliculatus (232)	0	11	2	8	58	14	1	6	0
Heterotrissocladius changi (91)	60	0	2	1	2	1	10	17	7
Ablabesmyia mallochi (94)	63	3	3	4	2	2	17	4	2
Trissopelopia ogemawi (62)	6	7	14	16	20	6	3	22	6
Nanocladius sp.n.1 (53)	5	10	11	23	27	5	3	16	0

- continued

Table XVIII (cont'd)

Species	*Sediment*	*Sparganium*	*Potamogeton*	*Hippuris*	*Moss*	*Algae*	*Sponge*	*Wood*	*Leaves*
Cricotopus bicinctus (92)	1	14	23	22	12	20	1	6	1
Stempellina sp.n.1 (179)	89	6	5	0	0	0	0	0	0
Cricotopus sp.n. (801)	4	0	1	1	21	72	1	0	0
Polypedilum braseniae (219)	96	0	0	0	0	0	0	4	0
Cryptotendipes casuaria (254)	100	0	0	0	0	0	0	0	0
Paratendipes albimanus (245)	100	0	0	0	0	0	0	0	0
Paracladopelma undine (238)	99	0	0	0	0	0	1	0	0
Arctopelopia flavifrons (160)	5	2	6	1	47	9	5	25	0
Tanytarsus curticornis (51)	7	18	4	24	15	0	9	21	2
Microtendipes pedellus (92)	24	2	9	11	0	0	20	34	0
Cricotopus trifasciatus (360)	2	73	5	10	2	5	0	2	1
Diplocladius cultriger (327)	0	63	6	0	6	0	0	0	25
Limnophyes spatulosus (348)	0	3	0	2	70	1	1	21	2
Psectrocladius simulans (68)	8	4	8	25	16	18	2	19	0
Polypedilum scalaenum (70)	4	20	9	16	6	14	2	29	0
Labrundinia pilosella (135)	17	11	2	48	4	0	2	7	9

3) Hippuris:

Labrundinia pilosella (48%)

4) Moss:

Limnophyes spatulosus (70%), L. folliculatus (58%), Arctopelopia flavifrons (47%).

5) Algae:

Cricotopus sp. n. (72%).

Of the remaining 12 species, 11 occurred primarily in only two or three microhabitats: Corynoneura lobata: Sparganium (29%), Potamogeton (21%), leaves (21%), Cricotopus bicinctus: Potamogeton (23%), Hippuris (22%), algae (20%); Microtendipes pedellus: wood (34%), sponge (20%); Nanocladius sp. n. 1: moss (27%), Hippuris (23%); Parakiefferiella sp. n. 1: wood (39%), sponge (16%); Polypedilum scalaenum: wood (29%), Sparganium (20%); Psectrocladius simulans: Hippuris (25%), algae (18%); Rheotanytarsus distinctissima: Potamogeton (35%), Hippuris (26%); Tanytarsus curticornis: Hippuris (24%), wood (21%); T. dispar: sediment (36%), wood (23%); Trissopelopia ogemawi: wood (22%), moss (20%).

The chi-squared values listed in Table XVIII are based on a comparison of a species' observed percentage frequency distribution in the nine microhabitats with the frequency distribution for the total sample of 8,025 larvae (Table XVII, column A). This is based on the rationale that if a species occurs at random among the nine microhabitats then its percentage frequency distribution should be the same as for the total sample of larvae. The higher the chi-squared value, the greater is the degree of habitat selection exhibited by a species. Only one of the 32 species, Paramerina fragilis, was found to be a habitat generalist, occurring in the nine microhabitats in the same proportion as the sample of total larvae ($\chi^2 = 13.4$, $P > 5\%$). Cricotopus sp. n., with a chi-squared value of 801 ($P < 0.005\%$) was the greatest habitat specialist. It was the only species that was abundant on filamentous algae. This species' larval case was usually surrounded by a dense clump of algae, measuring 2-3 cm in diameter, and was easily spotted in the otherwise homogeneous strands of algae. If the four major taxonomic groups are compared, the 11 species of Orthocladiinae have the highest mean chi-squared value (236). This was followed by the Chironomini (8 species, mean $\chi^2 = 197$) and the Tanytarsini (7 species, mean $\chi^2 = 129$). While the larvae of the above three groups are predominantly case builders and detritivores, the larvae of Tanypodinae are free-living and primarily predaceous. This may explain the low mean chi-squared value (104) of the six Tanypodinae species, indicating that this group as a whole is one of habitat generalists rather than habitat specialists.

In three of the four groups of congeneric species there were noticeable habitat differences between species belonging to the same genus. Tanytarsus dispar had the second lowest chi-squared value but showed some selection for wood. T. limneticus occurred almost exclusively in the sediment, while T. curticornis selected Hippuris and wood. As mentioned, Cricotopus sp. n. was found predominantly on filamentous algae, while C. trifasciatus, which had the second highest chi-squared value, occurred predominantly on Potamogeton. C. bicinctus selected algae, Potamogeton and Hippuris. Limnophyes folliculatus and L. spatulosus both occurred primarily on moss, but L. folliculatus also selected algae, while L. spatulosus also selected wood. Only the three species of Stempellina showed no habitat differences, with 85% or more of the larvae of each species occurring in the sediment.

F. Temporal and Spatial Overlap

The percent overlap in the emergence periods of the adults (temporal overlap) and in the microhabitats of the larvae (spatial overlap) was calculated for all 496 pairwise combinations of the 32 species which were most abundant as adults (Table XIX). When these values are plotted in the form of frequency histograms (Fig. 45), the distributions are seen to be markedly skewed towards the lower values. The absolute values are not too important since they depend on the number of categories used in the calculations. For example, the mean habitat overlap, being based on nine categories (sediment, Sparganium, Potamogeton, Hippuris, moss,

TABLE XIX Percent overlap of emergence periods (upper, right-hand part of matrix) and of larval microhabitats (lower, left-hand part of matrix) among the 32 most abundant chironomid species in the Bigoray River. Numbers 1-32 in the first column and first row correspond to the following species:

1	*Tanytarsus* *dispar*	17	*Cricotopus* *bicinctus*
2	*Stempellina* *leptocelloides*	18	*Stempellina* sp. n. 1
3	*Larsia* *pallens*	19	*Cricotopus* sp. n.
4	*Rheotanytarsus* *distinctissima*	20	*Polypedilum* *braseniae*
5	*Paralauterborniella* *nigrohalterale*	21	*Cryptotendipes* *casuaria*
6	*Tanytarsus* *limneticus*	22	*Paratendipes* *albimanus*
7	*Paramerina* *fragilis*	23	*Paracladopelma* *undine*
8	*Corynoneura* *lobata*	24	*Arctopelopia* *flavifrons*
9	*Pagastiella* *ostansa*	25	*Tanytarsus* *curticornis*
10	*Parakiefferiella* sp.n.1	26	*Microtendipes* *pedellus*
11	*Stempellina* sp. n. 2	27	*Cricotopus* *trifasciatus*
12	*Limnophyes* *folliculatus*	28	*Diplocladius* *cultriger*
13	*Heterotrissocladius* *changi*	29	*Limnophyes* *spatulosus*
14	*Ablabesmyia* *mallochi*	30	*Psectrocladius* *simulans*
15	*Trissopelopia* *ogemawi*	31	*Polypedilum* *scalaenum*
16	*Nanocladius* sp. n. 1	32	*Labrundinia* *pilosella*

Species arranged in order of decreasing abundance.

- continued

Table XIX (cont'd)

Emergence overlap

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	--	64	7	17	46	29	56	19	7	33	68	25	51	70	18	35	16	45	19	61	4	17	50	0	47	5	17	0	1	21	14	77
2	48	--	15	32	54	29	69	31	13	46	62	25	43	59	30	62	42	50	33	51	5	13	50	3	51	10	31	0	5	29	16	67
3	49	91	--	7	20	26	25	17	65	13	9	25	0	17	44	19	17	17	0	17	23	5	30	18	28	23	0	0	18	2	52	4
4	50	17	20	--	14	19	38	44	7	23	9	28	14	21	13	42	31	33	37	7	8	13	14	5	16	11	35	0	6	29	12	25
5	38	86	86	8	--	30	37	20	29	53	39	30	22	63	50	34	17	33	14	54	22	17	59	0	51	11	13	0	2	16	33	49
6	42	89	91	13	92	--	40	62	18	63	26	40	21	36	18	35	22	67	11	13	37	49	40	23	18	31	7	0	31	20	40	56
7	75	44	46	58	36	42	--	41	16	39	41	39	51	48	23	58	40	60	41	52	9	19	47	11	44	16	36	0	12	33	24	56
8	41	11	14	59	3	10	52	--	13	25	10	56	16	25	15	47	36	37	35	11	11	11	17	14	17	18	48	3	13	53	18	30
9	37	86	87	7	98	92	34	2	--	19	4	19	2	29	41	9	6	10	0	13	48	11	20	0	18	5	0	0	1	5	59	11
10	59	18	17	47	5	12	53	44	4	--	42	37	25	53	40	41	30	50	12	19	32	33	57	12	24	23	12	0	12	19	38	44
11	38	87	86	15	92	92	43	10	91	7	--	9	26	56	32	33	19	37	9	43	4	16	45	1	37	7	8	0	3	15	8	50
12	31	7	10	41	2	6	37	34	1	30	9	--	19	33	22	41	65	34	17	13	19	15	21	52	15	58	20	1	45	24	23	28
13	62	63	69	19	61	68	57	22	61	39	60	13	--	41	4	35	11	46	24	41	3	13	25	4	26	4	19	31	2	19	15	43
14	56	75	76	26	65	71	54	21	64	39	66	18	82	--	33	35	21	41	19	45	31	17	45	0	41	9	18	0	1	25	34	65
15	69	19	20	65	8	15	62	56	7	68	13	50	38	29	--	20	14	17	3	22	13	12	49	1	55	9	4	0	2	9	43	31
16	62	18	18	70	7	11	63	50	6	61	14	59	30	26	83	--	48	51	30	26	5	15	38	18	35	17	45	1	18	25	10	45
17	46	12	14	76	3	8	57	64	2	48	10	54	15	21	64	68	--	29	25	11	4	5	21	53	16	59	24	0	55	18	8	27
18	43	92	91	18	90	94	51	21	89	15	89	8	69	71	23	16	13	--	24	25	19	42	44	11	34	21	22	0	9	22	27	58
19	19	8	7	22	5	8	16	10	5	15	4	38	10	11	33	33	36	5	--	23	2	1	13	0	16	1	62	0	0	39	3	21
20	40	85	89	10	96	92	38	5	96	7	91	4	64	67	10	9	5	89	4	--	4	1	43	0	53	2	18	0	1	8	16	37
21	36	85	86	6	98	91	34	1	99	3	91	0	60	63	6	5	1	89	4	96	--	27	8	0	5	5	2	0	2	7	35	28
22	36	85	86	6	98	91	34	1	99	3	91	0	60	63	6	5	1	89	4	96	100	--	24	0	13	6	0	0	1	11	33	28
23	37	86	87	7	98	92	34	2	100	4	91	1	61	64	7	6	2	89	4	96	99	99	--	5	55	11	8	0	6	18	24	63
24	51	19	15	34	7	11	34	23	6	50	6	67	33	23	64	64	37	11	37	9	5	5	5	--	0	86	0	1	93	0	0	1
25	61	18	21	66	9	14	65	52	8	67	16	43	40	34	74	76	61	19	22	11	7	7	7	52	--	4	13	0	1	15	30	41
26	72	37	37	34	25	29	54	30	25	74	26	19	54	54	53	46	30	31	7	28	24	24	24	53	54	--	0	0	76	0	7	12
27	24	11	13	34	4	8	36	55	2	29	11	30	11	19	34	36	40	14	11	4	2	2	2	18	39	21	--	0	0	61	0	19
28	14	8	5	24	2	5	30	61	0	19	9	13	11	10	19	22	27	20	7	0	0	0	0	13	30	8	71	--	0	0	0	0
29	38	4	7	26	2	7	27	21	1	36	3	71	24	15	50	50	26	5	24	4	0	0	0	77	44	26	11	11	--	0	1	3
30	64	20	21	64	10	14	60	41	9	63	12	51	33	28	77	79	72	17	41	12	8	8	8	59	75	50	30	16	42	--	10	40
31	60	16	17	53	6	10	57	58	5	71	13	48	29	24	72	68	67	15	27	8	4	4	4	54	71	57	46	32	34	73	--	19
32	47	23	29	56	19	25	68	49	18	43	26	32	38	36	50	53	48	34	11	21	17	17	17	22	59	46	30	26	19	52	46	--

Habitat overlap

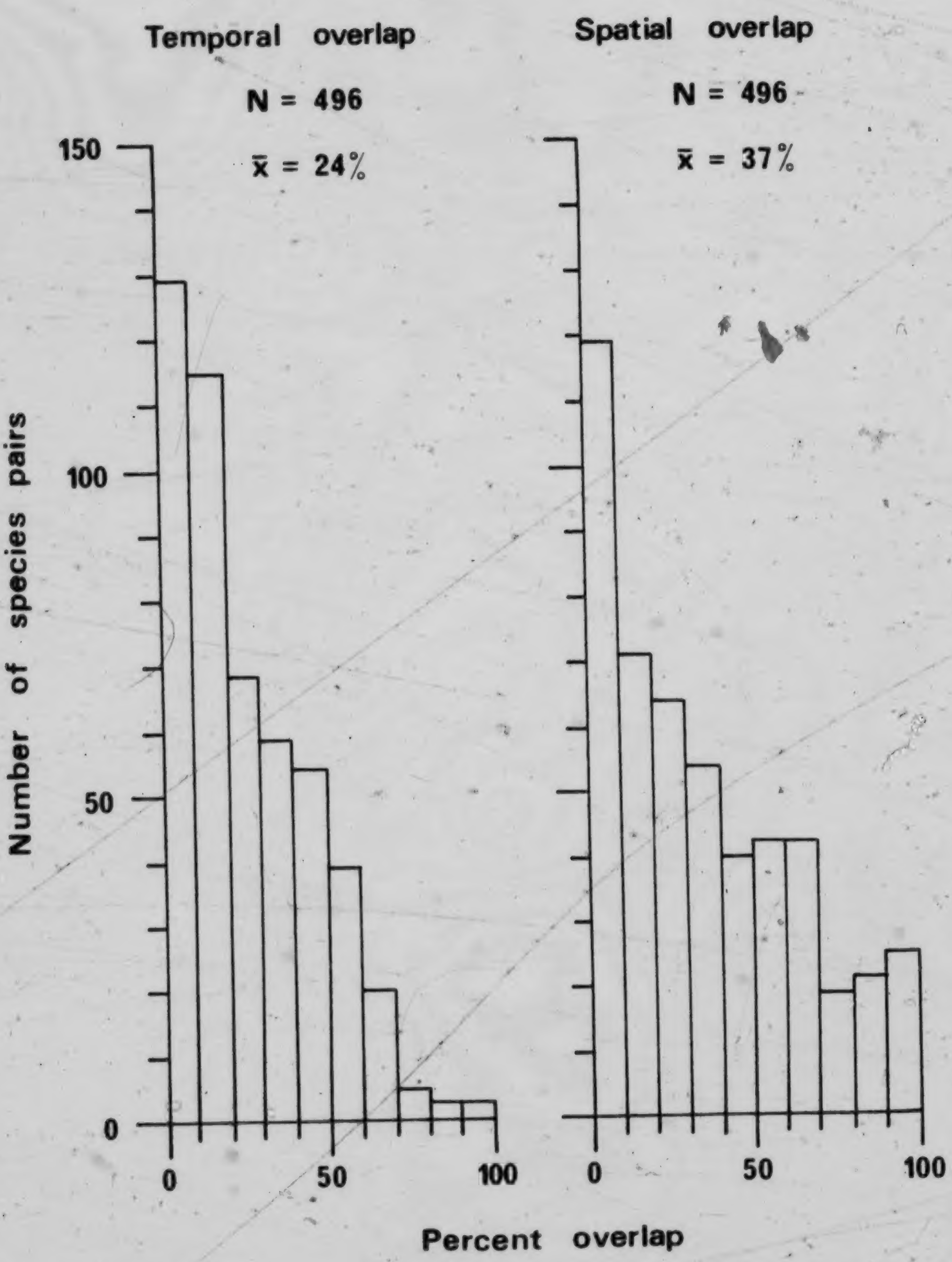

Fig. 45. Variation in percent temporal and spatial overlap between 32 commonest chironomid species in the Bigoray River.

algae, sponge, wood and leaves), is much higher than temporal overlap, which is based on 36 time intervals (p.38). Overlap values can, however, be used to make some interesting comparisons, such as seasonal changes in temporal overlap, effect of different microhabitat types on spatial overlap, comparison of overlap values of the four major taxonomic groups, comparison of species belonging to different trophic levels, and the relationship between spatial and temporal overlap.

When mean temporal overlap is calculated for each of the 36 sampling intervals, it varied erratically from 0.1% to 7.3% throughout the emergence season, with no particular seasonal trend (Figure 46). In other words, there is no indication that the emergence periods of the 32 most abundant species overlapped more during the middle of the emergence season, when many species were emerging, than earlier or later in the year, when only a few species were emerging. This might indicate the existence of a mechanism, such as the interplay between intra- and interspecific competition, which maintains emergence overlap at the same level throughout the emergence season.

Larvae showed much greater overlap in the sediment than in any of the other eight microhabitats (Table XX). If the sediment category had been further subdivided according to particle size and organic content, the overlap values would quite likely be similar to values for other microhabi-

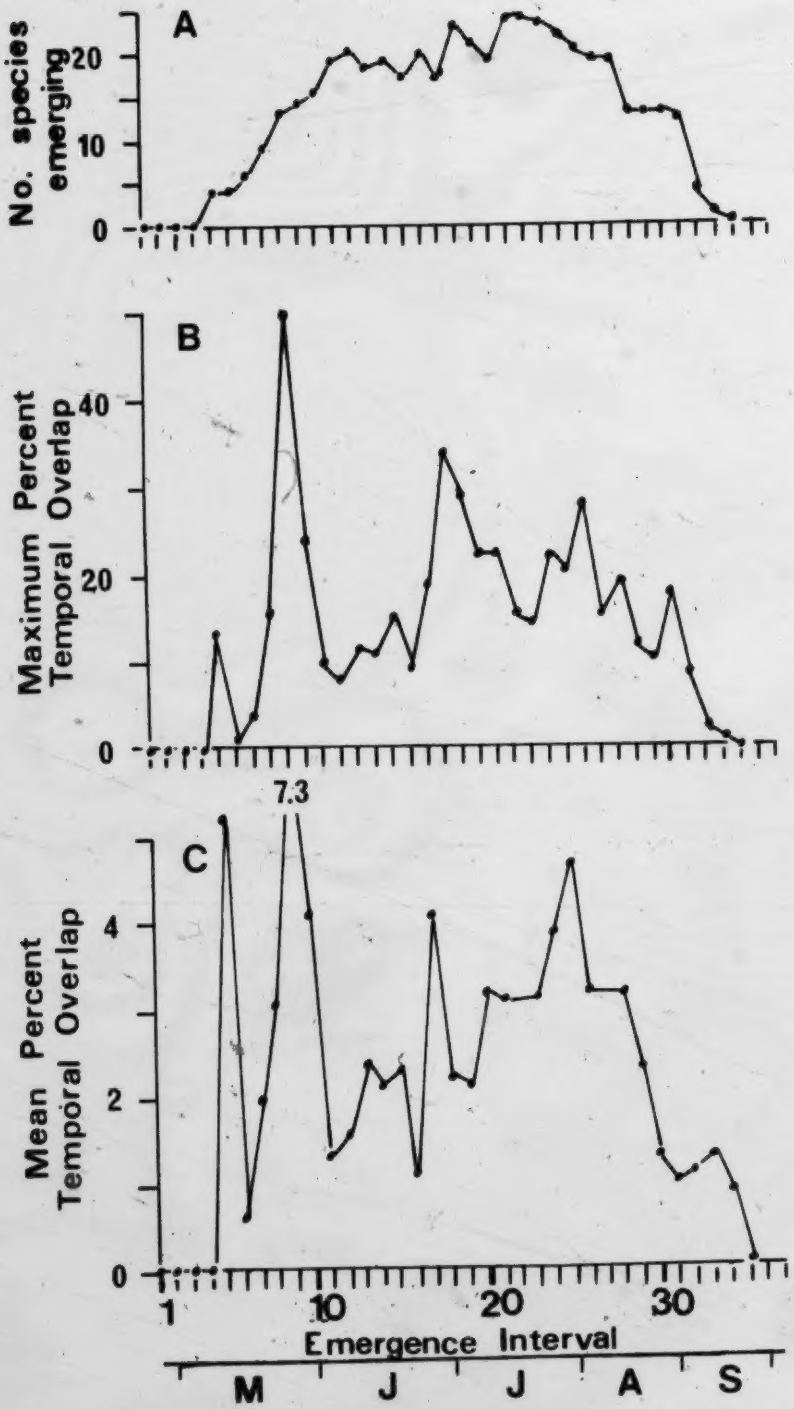

Fig. 46 Seasonal changes in numbers of emerging species (A), maximum percent temporal overlap (B), and mean percent temporal overlap (C). Data refer only to 32 commonest chironomid species in the Bigoray River, based on emergence studies.

TABLE XX Percent overlap of chironomid larvae in different microhabitats in the Bigoray River. Data include 32 commonest species based on emergence data. Means are based on 496 species pairs.

Microhabitat	Mean overlap	Range
Sediment	15%	0-100%
Sparganium	3%	0- 63%
Potamogeton	2%	0- 23%
Hippuris	7%	0- 26%
Moss	3%	0- 58%
Fil. algae	1%	0- 20%
Sponge	1%	0- 20%
Wood	3%	0- 34%
Leaves	2%	0- 29%
All microhabitats	37%	0-100%

tats. Larvae therefore appear to subdivide the sediment into a number of microhabitat types possibly based on variations in particle size and organic content. I did not have time to determine how different sediment types were partitioned among the various species, although sediment analysis (p.22) did indicate variations both in particle size and organic content. Overlap values for the remaining eight microhabitats should be comparable, and indicate that overlap on the finely-divided Hippuris leaves is 2-3 times higher than in the other non-sediment microhabitats.

Examination of gut contents of mounted larvae of the 32 commonest species indicated that the six species of Tanypodinae were all predators, while the remaining 26 species were either herbivores or detritivores. Temporal and spatial overlap for the 135 species pairs, composed of one Tanypodinae and one non-Tanypodinae, averaged higher than for the 365 species pairs in which both members belonged to the same trophic level (Table XXI). Since a large percentage of the food of Tanypodinae is composed of other chironomid larvae (Morgan 1949), the high spatial overlap between Tanypodinae and other chironomids probably results from the association of a predator with its prey.

Spatial and temporal overlap was much higher between congeneric species than between species belonging to different genera (Table XXI). Among the 32 most abundant species, there were 5 genera with two or more species: Tanytarsus dis-

TABLE XXI Comparison of mean temporal and mean spatial overlap between various taxonomic and ecological groupings of the 32 most abundant species in the Bigoray River.

	Type of comparison	No. of pairs	Mean temporal overlap (%)	Mean spatial overlap (%)
A.	Between congeners	11	38	50
	Between non-congeners	485	24	36
B.	Between 11 species of Orthocladiinae	55	24	42
	Between 6 species of Tanypodinae	15	25	42
	Between 8 species of Chironomini	28	23	61
	Between 7 species of Tanytarsini	21	38	49
C.	Between species from different trophic levels	135	30	48
	Between species from same trophic level	361	22	33

par, *T*. *limneticus*, *T*. *curticornis*, *Stempellina leptocelloides*, *S*. sp. n. 1, *S*. sp. n. 2, *Limnophyes folliculatus*, *L*. *spatulosus*, *Cricotopus bicinctus*, *C*. sp. n., *C*. *trifasciatus*, *Polypedilum braseniae* and *P*. *scalaenum*.

Temporal overlap between Tanytarsini species was higher than between species of Orthocladiinae, Tanypodinae, or Chironomini (Table XXI). The Tanytarsini were the most abundant group in the Bigoray River, and initially I felt that this might have had some bearing on the high temporal overlap values of this group. There was, however, no relationship between the temporal overlap of a pair of species and the abundance of each species (Table XXII). Mean overlap values between very abundant species were as high as between less abundant species. Furthermore, there was no relationship between the abundance of a species and its mean temporal overlap with the other 31 species (Table XII, p.77).

The high spatial overlap between species of Chironomini is quite likely an overestimate. Chironomini larvae occurred primarily in the sediment (Table XVII, p.115). This was treated as a single microhabitat in my study, but Table XX, (p.127) suggests that the larvae subdivided the sediment into a number of microhabitats.

Pairs of species having high temporal overlap generally also exhibited high spatial overlap. A significant correlation ($P < 5\%$) between temporal and spatial overlap

TABLE XXII Mean percent temporal overlap between pairs of species whose members belong to various abundance categories: high (427 - 1,480 males/m^2/yr), medium (120 - 352), low (49 - 86). Number in brackets indicates the number of pairs.

Abundance of first member of a pair	Abundance of second member of a pair		
	High	Medium	Low
High	23 (6)	--	--
Medium	31 (44)	32 (55)	--
Low	23 (68)	24 (187)	18 (136)

was observed among all 32 species when treated together (Fig. 47), and among the Tanytarsini (Fig. 48). The trend was also apparent among the other three groups (Tanypodinae, Orthocladiinae, and Chironomini), and lack of statistical significance (P > 5%) probably resulted from small sample sizes (Fig. 48).

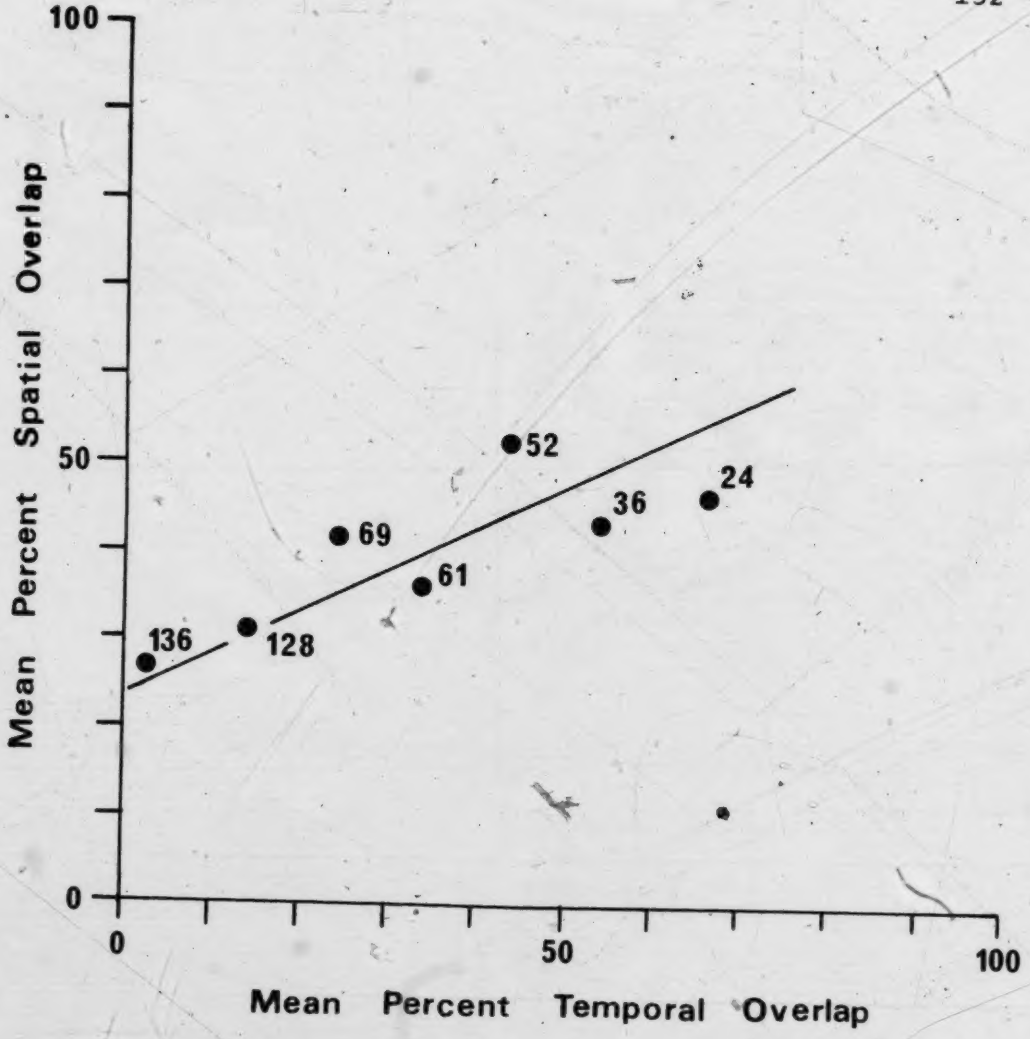

Fig. 47 Relationship between temporal and spatial overlap among 32 most common chironomid species in the Bigoray River. Points are means based on grouped data, with the number of values in each group indicated beside each point. Regression equation is $Y = 29.3 + 0.3X$, $r = 0.78$, $P < 5\%$.

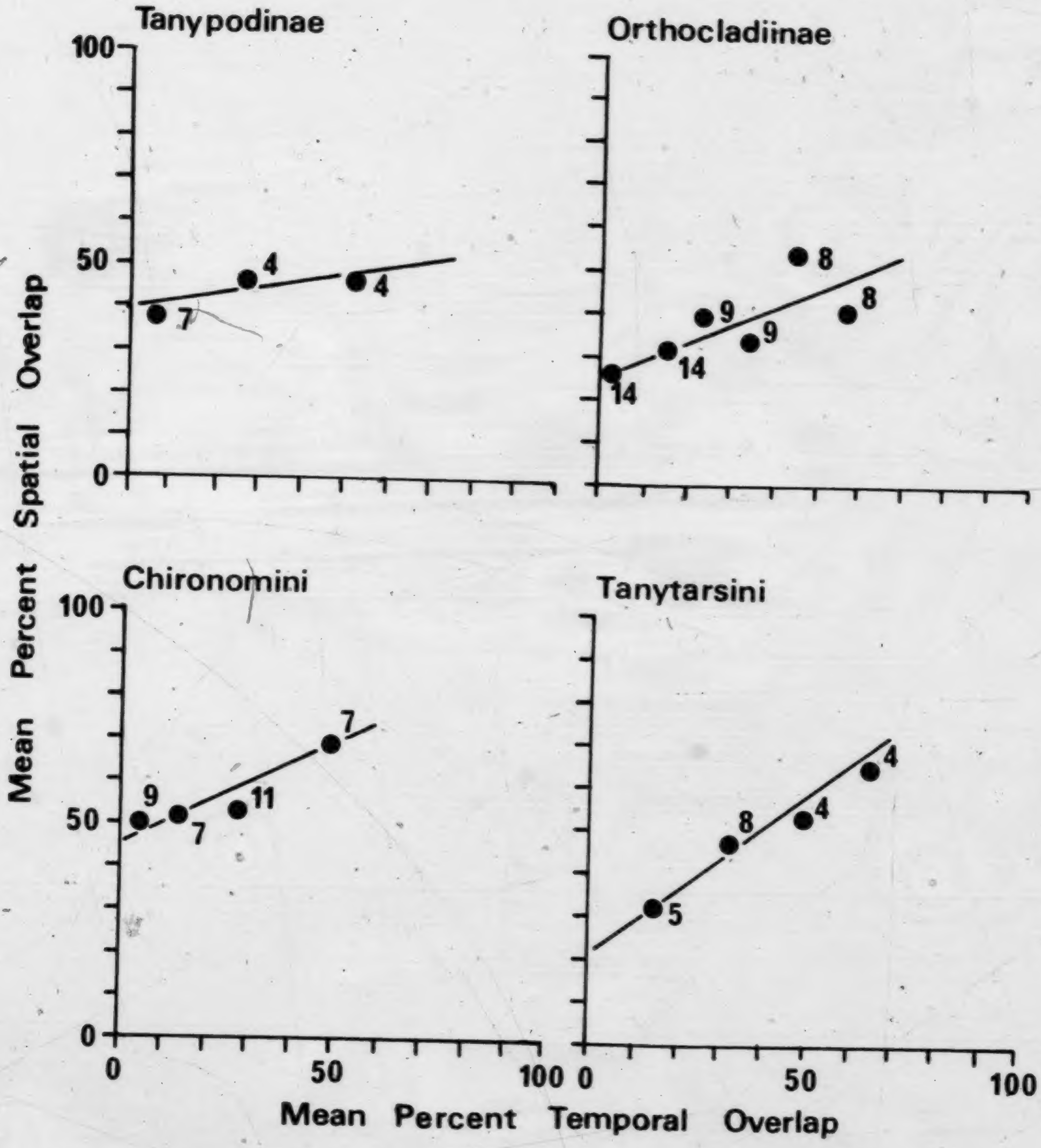

Fig. 48 Relationship between temporal and spatial overlap between species of Tanypodinae (r = 0.68, P > 5%), Orthocladiinae (r = 0.71, P > 5%), Chironomini (r = 0.91, P > 5%), and Tanytarsini (r = 0.99, P < 5%). Points are means based on grouped data, with number of values in each group indicated beside each point.

V. DISCUSSION AND CONCLUSIONS

A. Comparison of the Bigoray River Chironomid Fauna with that of Other Streams

The 112 species of Chironomidae collected from the 150-m section of the Bigoray River appears to be the highest number ever recorded from such a small area. Wilson (1977) recorded 86 species from a single station on the River Chew, England, (drift netting pupal exuviae), and Pinder (1974) collected 75 species from a single site on a small English chalk stream (collecting adults with sticky traps). Illies (1971) collected 70 species from a single site on the Breitenbach, West Germany, by covering a 10-m stream section with a greenhouse and collecting all adults emerging within it. Coffman (1973) recorded 142 species from Linesville Creek, Pennsylvania, but this number is not strictly comparable with that from the Bigoray River, since Coffman's study area extended over 1 km of stream. Similarly, the 246 species recorded by Lehmann (1971) from the River Fulda, West Germany, were collected throughout the whole 200-km length of the river. Although Lehmann does not actually mention the number of species recorded from individual sites, his data suggest that some of the sites had close to, if not over, 100 species.

The large number of chironomid species recorded from the Bigoray River study area may be partly due to a beaver dam located approximately 500 m upstream. At the dam, and for a short distance below it, the current is very fast. Chironomid larvae from this section could have been swept downstream into my study area, especially during periods of high water. This would also explain why more rare species were collected than were expected, based on the log-normal distribution. It would also explain why many of the less abundant species were Orthocladiinae that are normally found in faster-flowing water.

Visits to numerous points along the Bigoray River, as well as examination of aerial photographs, indicated the frequent occurrence of beaver dams along the stream's entire course. As one proceeds downstream from one beaver dam to the next, there is a reduction in current velocity, an increase in water depth, and an increase in the depth of silt deposited on the river's bottom. The pond-like area just upstream from a dam was found to be up to 3 m deep. This gradation of environmental factors can be repeated many times within relatively short distances, since dams have been found as close together as 500 m in the Bigoray River. Although I never checked whether there was longitudinal zonation of species between dams, I strongly suspect this to be the case. This supposition is based on the results of the microhabitat studies showing that larvae of most chironomid species had fairly restricted distribution patterns within the study area. Sprules (1941) also showed that increased amount of bottom silt resulting from building of a new beaver dam greatly influenced the abundance of insects living there. If such repetitive patterns of longitudinal zonation exist, then study areas on the Bigoray River and similar streams should in future be large enough to at least include the distance between two dams. Results from smaller study areas will be difficult to compare since composition of the chironomid community will depend in part on where the study area is located in relation to beaver dams. Studies carried out just upstream of dams will probably show high percentages of Chironomini, while studies conducted just downstream from dams will show high percentages of Orthocladiinae.

One way of comparing the chironomid fauna of the Bigoray River with that of other streams is to tabulate the percentage of the total species belonging to each of the four major taxonomic groups (Table XXIII). Streams having less than 30 species were most likely not studied in sufficient detail and were excluded from the table. Streams have been arranged in order of decreasing percentage of Orthocladiinae, partly because abundance of this group varied the most among streams (22-90%), and because Thienemann (1954) showed that the percentage of Orthocladiinae species decreases as one moves from fast-flowing mountain streams to slow-moving lowland streams. This trend is also seen in Table XXIII, the first three streams being mountain streams and the last 12 being lowland streams and rivers. Furthermore, as percentage of Orthocladiinae decreases there is a concomitant in-

TABLE XXIII Percent abundance of species of Tanypodinae (Tp), Orthocladiinae (Or), Chironomini (Ch) and Tanytarsini (Tt) in various streams. Podonominae and Diamesinae included with Orthocladiinae. N = total number of species.

	Stream	N	Tp	Or	Ch	Tt
1.	High Tatra streams, Poland (Kownacki and Kownacka 1971)	42	5	90	0	5
2.	Alps, several streams (Thienemann 1954)	64	8	81	2	9
3.	Mittelgebürge, W. Germany (Thienemann 1954)	89	9	70	10	11
4.	R. Dodder, Ireland (Fahy and Murray 1972)	67	12	67	15	6
5.	Altahoney R., Ireland (Fahy and Murray 1972)	54	14	66	10	10
6.	Danube R., Czechoslovakia (Ertlova 1970)	40	3	65	27	5
7.	Aabach, W. Germany (Dittmar 1955)	64	8	59	14	19
8.	R. Endrick, Scotland (Maitland 1966)	39	5	59	23	13
9.	Linesville Cr., Pennsylvania (Coffman 1973)	143	10	58	17	15
10.	Fulda, W. Germany (Lehmann 1971)	249	11	58	14	17
11.	Tadnall Brook, England (Pinder 1974)	75	9	56	16	19
12.	Danube R., Hungary (Berczik 1971)	30	3	50	40	7
13.	Great Berg R., S. Africa (Scott 1958)	83	13	46	30	11

- continued

Table XXIII (cont'd)

	Stream	N	Tp	Or	Ch	Tt
14.	R. Chew, England (Wilson 1977)	86	19	44	24	13
15.	Bigoray R., Alberta (this study)	112	18	43	20	19
16.	Susa, Denmark (Berg 1948)	84	18	43	24	15
17.	Hamble R., England (Hall 1960)	50	12	42	24	22
18.	Kossau, W. Germany (Nietzke 1937)	79	15	39	18	28
19.	Doulonnes, France (Verneaux 1968)	48	19	37	27	17
20.	Savannah R., S. Carolina (Roback 1953)	69	19	33	39	9
21.	Danube R., Rumania (Cure 1964)	63	7	32	52	8
22.	Saan, Poland (Zacwilichowska 1970)	35	14	32	37	17
23.	Oder, E. Germany (Harnish 1922)	60	15	30	45	10
24.	Lytle Cr., Ohio (Paine and Gaufin 1956)	63	24	28	40	8
25.	Hunt Cr., Michigan (Curry 1954)	36	22	22	31	25

crease in percentage of Chironomini (Fig. 49). Tanypodinae comprise 3-24% of the chironomid species in streams and Tanytarsini comprise 5-28%. Both groups appear to be somewhat more abundant in lowland than in mountain streams.

Of the rivers listed in Table XXIII, the River Susa, Denmark, had the chironomid fauna with the greatest similarity to that of the Bigoray River. Four other streams - Chew, Hamble, Kossau and Doulannes - had chironomid faunas which were also quite similar to that of the Bigoray River. These six are all small, slow-flowing, lowland streams with silt and sand substrates, and with a varying amount of aquatic macrophytes. Of the 24 common genera in the Bigoray River (i.e., those containing the 32 most abundant species), 50% or more were also found in each of the other five streams. Furthermore, Holarctic species that were common in the Bigoray River (e.g., Polypedilum scalaenum, Microtendipes pedellus, Paratendipes albimanus and Cricotopus bicinctus), were also abundant in most of the other five streams.

The six streams discussed above extend over 10° latitude (43°N - 53°N), are located in a variety of climatic regions (i.e., 0-6 months of ice cover), and flow through either coniferous or deciduous forests. The composition of other invertebrate groups in the River Kossau and Susa is also similar to that in the Bigoray River. Data on other groups are not available for the Doulonnes, Chew and Hamble Rivers. There is therefore a good indication that small, slow-flowing

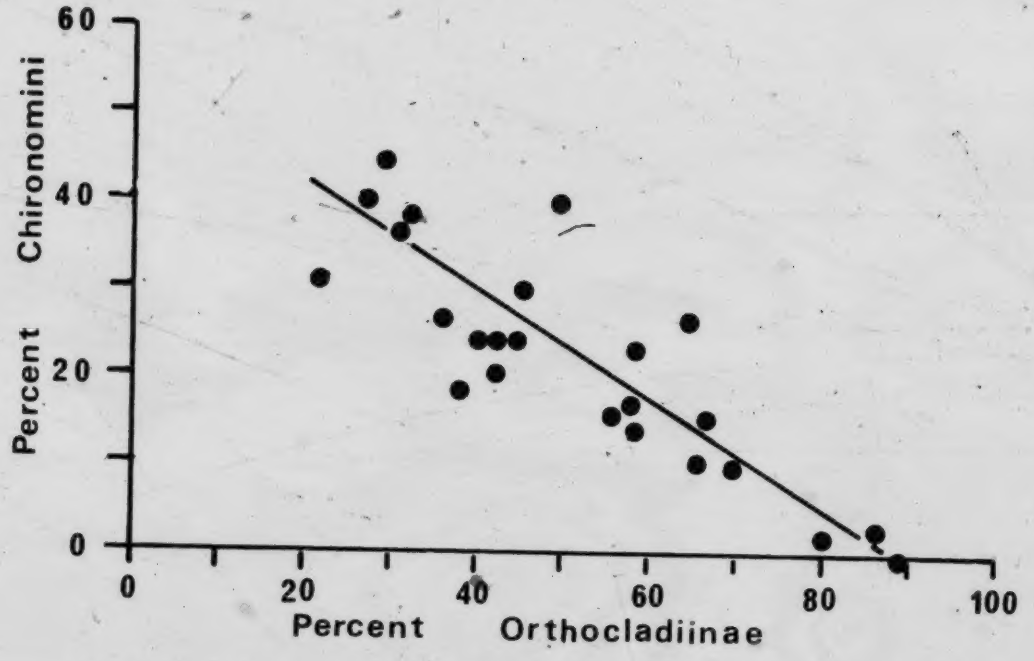

Fig. 49 Relationship between percent abundance of Orthocladiinae and Chironomini species in 25 streams. Regression equation is $Y = 55 - 0.6X$, $r = -0.82$, $P < 1\%$.

lowland streams represent as uniform and distinct a category of streams as torrential mountain streams, whose remarkable similarity the world over has been documented by Hynes (1970).

B. Microhabitat Distribution of Larvae

The similarity of the chironomid fauna of slow-flowing lowland streams is most likely due to similar substrates. Hynes (1970) states that substratum is the major factor controlling the occurrence of stream invertebrates, and he cites numerous studies from all parts of the world that show that as the substrate changes from place to place so does the fauna. My larval microdistribution data for the 32 most abundant chironomid species showed that only one species, *Paramerina fragilis*, a free-living predator, was a habitat generalist. It occurred in the nine microhabitats in the same proportions as the total sample of 8,025 larvae. Larvae of the remaining species occurred primarily either in one microhabitat (20 species), two microhabitats (9 species), or three microhabitats (2 species).

It seems reasonable to assume that species which are restricted to a few microhabitats (i.e., habitat specialists) should be less abundant than species which occur in a variety of microhabitats (i.e., habitat generalists). When abundance (males/m^2/year) of the 32 most common chironomid species is plotted against habitat selectivity (as measured by the χ^2

values in Table XVIII, p.116), a weak inverse relationship (r = -0.23) can indeed be observed between the two parameters. The correlation is, however, not statistically significant (P > 5%).

The long strands of filamentous algae that occurred primarily in spring and late summer were probably the most ephemeral of the nine microhabitats. Yet this was the only microhabitat from which I collected *Cricotopus* sp. n. *Cricotopus bicinctus* and *Psectrocladius simulans* also selected algae as one of their microhabitats. Associations between filamentous algae and chironomid larvae, especially *Cricotopus*, have been noted in other studies (Meuche 1939, Mundie 1957, Darby 1962). *Cricotopus nostocicola* parasitizes the spherical colonies of the blue-green alga *Nostoc* (Brock 1960). The larvae of some species of *Psectrocladius* are known to use filamentous algae, especially *Spirogyra*, both for food and case construction (Thienemann 1954).

Colonies of green sponge (*Spongilla* sp.) formed a distinctive microhabitat, but these colonies were not abundant in the Bigoray River. *Xenolabis xenolabis*, a chironomid whose larvae live inside freshwater sponges (Pagast 1934, Wundsch 1943, Roback 1968), was rarely found. Larvae of the Spongilla fly, *Climacia* sp. (Neuroptera: Sisyridae), was the only invertebrate that commonly occurred in or on the sponge colonies.

Submerged branches and tree trunks were common in the

Bigoray River due to the easily eroded banks and the activity of beavers. Wood provided a distinctive substrate except when covered by moss, filamentous algae or sponge, and was the preferred microhabitat of *Mictotendipes pedellus*, *Parakiefferiella* sp. n. 1, *Polypedilum scalaenum*, *Tanytarsus curticornis*, *T. dispar* and *Trissopelopia ogemawi*. However, all of the above species also selected one other microhabitat. Of the above species, only *Polypedilum* has been reported to frequent and even feed on wood (Shadin 1956, quoted in Hynes 1970). However, *Glyptotendipes*, the genus most commonly reported mining in decaying wood, was never found in the Bigoray River.

Moss was the preferred microhabitat of only three species, and one of two preferred microhabitats of two other species. *Limnophyes folliculatus* and *L. spatulosus* showed the highest preference for moss, a habitat from which the genus has been frequently reported. Humphries and Frost (1937) found larvae of an unidentified *Limnophyes* species to be abundant on moss in the River Liffey, Ireland. Reiss (1968) lists *L. prolongatus* and *L. pusillus* as belonging to the characteristic species of moss.

Potamogeton was preferentially colonized by four species, but these species also selected other microhabitats. Two of the genera, *Cricotopus* and *Polypedilum*, have been reported to mine and channel into the leaves of *Potamogeton* (Berg 1950, Matlak 1963). *Corynoneura* was not mentioned as occurring on *Potamogeton* by Berg, possibly because the larvae are free-living and easily lost when collecting plants unless proper precautions are taken. Goetghebuer (1932) lists the underside of *Nuphar* and *Potamogeton* as the microhabitat of *Corynoneura*. Darby (1962) found them abundant on unnamed species of aquatic macrophytes in California rice fields. Matlak (1963) found *Corynoneura* abundant on *Potamogeton* in Polish carp ponds, and Stimac and Leong (1977) found them abundant on *Potamogeton* in a shallow California lake

Rheotanytarsus distinctissima, the fourth species to occur on *Potamogeton*, builds unique, hydra-shaped cases. Walshe (1950) and Scott (1967) have shown that the larvae spin silken nets between the arms extending outward from the cases. The net filters small detritus particles from water, and periodically a section of the net is rolled up by the larvae and eaten. A new net is then spun to replace the old one.

In the Bigoray River, autumn-shed leaves were preferentially colonized by *Corynoneura lobata* and *Diplocladius cultriger*, but leaves were not the only preferred habitat of these two species. *Diplocladius cultriger*, as well as *Cricotopus trifasciatus* also selected *Sparganium*. However, I have not been able to find references to chironomids inhabiting leaves and *Sparganium* in other streams.

The 13 species showing a preference for sediment (p. 116) belonged to 11 genera (*Ablabesmyia*, *Cryptotendipes*, *Heterotrissocladius*, *Larsia*, *Pagastiella*, *Paracladopelma*, *Paralauterborniella*, *Paratendipes*, *Polypedilum*, *Stempellina* and *Tanytarsus*) which have been frequently recorded from the littoral sediments of lakes. For example, Brundin (1949) recorded all of the above genera except *Larsia* from littoral sediments of Swedish lakes. Reiss (1968) lists these genera, except *Larsia* and *Pagastiella*, from littoral sediments of Lake Constance, West Germany. Hamilton (1965) found all above genera except *Cryptotendipes*, *Paracladopelma*, *Paralauterborniella* and *Paratendipes* in littoral sediments of Marion Lake, British Columbia.

Initially, I had planned to subdivide the sediment into a number of categories based on particle size and organic content, but abandoned the idea after realizing the large amount of time required for such a detailed analysis. Furthermore, results of the preliminary sediment analysis (p.19) indicated the bottom to be fairly uniform. For example, mean particle size of 73 core samples ranged from 0.06 mm (very fine sand) to 0.98 mm (coarse sand). Although the 16 times difference in the two sizes now seems large, the fact that they were all classified as sand, rather than sand, silt and clay, led me to believe that chironomid larvae would not discriminate between such a small range of particle sizes. Although organic content of the sediment varied from 1-60%, over three-quarters of the samples had an organic content of 3-7%. Again, I felt that this indicated fairly uniform conditions. Furthermore, Wene (1940) could find no correlation between chironomid larval density and organic content of the sediment. Similarly, McLachlan and McLachlan (1971) could find no correlation between chironomid biomass and percentage of organic carbon in the littoral sediments of Lake Kariba, Rhodesia. They also could find no difference between the chironomid biomass of a station with 1% coarse sand and a station with 48% sand. A third station, with 69% coarse sand, had only a quarter of the chironomid biomass of the other two stations; but only a few of the sediment samples from the Bigoray River contained such a high percentage of coarse sand.

The large number of species that were found in sediment, as well as much higher overlap between species in this microhabitat when compared to others, now suggests that chironomid larvae do discriminate between various sediment types. This is a topic needing further investigation. It is, of course, possible that this discrimination is not so much based on particle size and organic content, parameters that are comparatively easy to measure, as it is on composition and abundance of the microbial fauna, as has been found in tubificid oligochaetes (Brinkhurst et al. 1972).

Since many of the sediment-inhabiting larvae are burrowers, surface compaction might also be important in explaining patterns of microdistribution among different species. For example, Ford (1962) found a significant correlation between density of the surface layers of mud in a stream and horizontal distribution of chironomid larvae.

Very little is also known about the mechanism whereby chironomid larvae select certain aquatic plants. The shape and surface texture of leaves and stems, as well as the growth form of the plants certainly play a role, since they determine how effectively larvae will be able to move about the plant (or mine within it, as do some chironomids), how much protection they will receive from the current, and also how much detritus will be deposited on the surface of the plant. For example, upper surfaces of Potamogeton leaves were often observed to be coated with a flocculent deposit of marl through which larvae could move easily. The marl also trapped large quantities of detritus. Species composition and abundance of epiphytic algae and other microorganisms on macrophytes quite likely also play a role in selection of plants by larvae. Differences in epiphytic algae of aquatic plants have been reported by Harrod (1964). The chemical nature of plants may also be involved. Emergence of mosquito larvae has been shown to be influenced by plant auxins (Abdel-Malek 1948), and Edmondson (1944) showed that the sessile rotifer Collotheca avoids Chara because of volatile substances produced by the plant.

C. Temporal and Spatial Variation in Larval Density

Only a few values have been published on the abundance of chironomid larvae on aquatic macrophytes. In an English chalk stream Harrod (1964) found an average of 50, 74 and 120 larvae/1,000 cm^2 of plant surface on *Callitriche*, *Carex* and *Ranunculus*, respectively. In Lake Balaton, Hungary, Entz (1947) found 160 and 185 larvae/1,000 cm^2 on *Myriophyllum* and *Potamogeton*, respectively. These values are similar to the average values of 131, 166 and 183 larvae/1,000 cm^2 recorded from *Sparganium*, *Potamogeton* and *Hippuris*, respectively, in the Bigoray River. The average density of 447 larvae/gm dry weight of *Myriophyllum* found by Petr (1968) in Lake Volta, Ghana, is also similar to the average density of 466 larvae/gm dry weight of *Hippuris* in the Bigoray River. *Hippuris* is used for comparison here because, of all aquatic plants in the Bigoray River, it is closest in growth form to that of *Myriophyllum*. Matlak (1963) found that aquatic plants in several Polish carp ponds supported 0.3×10^3 to 51.9×10^3 larvae/liter of plant volume, with values increasing from May to September. These values again are similar to those recorded throughout the summer in the Bigoray River: 1.1×10^3 to 18.9×10^3 larvae/liter for *Sparganium*, 3.8×10^3 to 27.0×10^3 larvae/liter for *Potamogeton*, and 8.4×10^3 to 47.1×10^3 larvae/liter for *Hippuris*. Bownik (1970) measured the abundance of chironomid larvae on *Myriophyllum*, *Elodea* and *Potamogeton* in another Polish lake, and Mrachek (1966) lists the abundance of larvae on 11 species of aquatic plants in Clear Lake, Iowa. However, both these authors expressed larval densities in terms of fresh weight of plants, making comparison with my results difficult. If one assumes that a plant's dry weight represents 10% of its fresh weight, then these values would fall within the range of values found in the Bigoray River.

Comparison of Table VI (p.33) with Table XV (p.107) shows that plants with large surface area per unit weight, e.g., Hippuris, were colonized by more larvae than plants with small surface area per unit weight, e.g., Sparganium. A similar correlation between plant surface area and larval density has been reported by Krecker (1939), Rosine (1955) and Mrachek (1966). This relationship indicates that aquatic plants serve primarily as substrates for invertebrates rather than as a direct source of food. This is also suggested by the similarity of the species composition and relative abundance of invertebrates on real plants as compared with those on artificial plants made from plastic (Egglishaw 1964, Glime and Clemens 1972).

The density of larvae on submerged wood in the Bigoray River also compares well with published values. Nilsen and Larimore (1973) found an average of 14 x 10^3 chironomid larvae/m^2 on submerged logs in a river in Illinois during late September. At this time in the Bigoray River the mean density of larvae on submerged wood was 16 x 10^3 larvae/m^2. Claflin (1968) found a maximum of 11 x 10^3 larvae/m^2 on submerged trees in the Lewis and Clark Reservoir, South Dakota.

I was not able to find published values on chironomid larval densities on either moss or filamentous algae.

Glime and Clemens (1972) showed that chironomid larvae were very abundant on moss as I found in the Bigoray River, but they do not give data on number of larvae per unit of plant.

In the Bigoray River, density of chironomid larvae on sediment averaged 20 x 10^3 larvae/m^2 over the 23-month study period, with maximum density being 53 x 10^3 larvae/m^2 (Oct. 1, 1973). Although these densities appear high, maximum values as high or higher have been reported by other authors. For example, Jonasson (1972) reported a maximum of 70 x 10^3 larvae/m^2 for one station (Skovlund) in Lake Esrom, Denmark. Mundie (1957) recorded a maximum of 47 x 10^3 larvae/m^2 in an English Reservoir. McLusky and McFarlane (1972) recorded maximum densities of 30 x 10^3 larvae/m^2 in Loch Leven, Scotland. Knauss (1970) and Topping (1971) list densities of 30 x 10^3 larvae/m^2 for saline lakes in South Dakota and British Columbia, respectively. Numerous other values on the density of chironomid larvae inhabiting bottom sediments can be found in the literature, many reporting maximum densities less than 1 x 10^3 larvae/m^2. I feel that in most cases these low maximum values reflect inefficient sampling techniques, instead of absolute low densities of chironomids.

Exceptionally high densities of 100 x 10^3 larvae/m^2 have been achieved by culturing Chironomus larvae in the laboratory (Konstantinov 1958). Densities of 250 x 10^3 larvae/m^2 have been reported by Lindegaard and Jonasson (1975) from Lake Myvaten, Iceland. "My" is the Icelandic word for midges, and the lake is famous for the huge swarms of these flies that form above the lake each summer. At this density the mean area per larvae is only 4 mm^2, or about the size of the following circle "o".

In the Bigoray River, total density of chironomid larvae in the sediment was lowest in June and highest in March. Similar patterns of seasonal change, characterized by summer minima and winter maxima in larval density, have been reported in shallow, temperate lakes by Mundie (1957), Hamilton (1965), Armitage (1970) and Knauss (1970). However, Maitland (1966) found that in the River Endrick, Scotland, density of chironomid larvae was lowest in winter and highest in summer.

In the Bigoray River, minimum density of larvae in sediment during June resulted both from emergence of adults from the river and from larvae colonizing new growths of aquatic macrophytes appearing in June. These plants increased the total surface area available for colonization by ten times. As shown in Table XV (p.107), density of larvae on Sparganium, Potamogeton and Hippuris generally increased from June 11 to October 1, 1973. Similar increases in density of chironomid larvae on aquatic plants have been reported by Matlak (1963), Harrod (1964) and Bownik (1970), and probably occur on all aquatic macrophytes that die back during winter and then start growing again the following summer. Such seasonal changes are not seen on plants, such as moss, persisting throughout the year.

Experiments with the wire mesh cages indicated a gradual decomposition of aquatic macrophytes during winter. The resulting reduction in total surface area probably led to increased density of larvae in the sediment during winter. Immigration of larvae from upstream areas or delayed hatching of eggs could also have led to an increase in larvae during winter. Life history data, however, indicated that larvae of all species were present at the start of winter, and sediment samples taken at different stations did not indicate any major population shifts.

D. Life Histories

Of the 32 chironomid species for which life history data was collected, 47% were bivoltine, 34% were univoltine, and 19% were trivoltine. Hamilton (1965) however, found that most species living in Marion Lake, British Columbia, were univoltine, and a similar conclusion was reached by Miller (1941) for Costello Lake, Ontario. The large number of multivoltine species in the Bigoray River is therefore somewhat surprising, especially since the total degree-days for the stream (2,000) is lower than for either Marion Lake (3,000) or Costello Lake (2,800). Learner and Potter (1974) found more bivoltine than univoltine species in two shallow ponds in England, but this would be expected since the total degree-days recorded for the ponds was 3,500. It is unlikely that other environmental factors (e.g. food) exerted as great an influence as temperature on the rate of development of chironomid larvae in the above water bodies.

Comparison of the species composition of the Bigoray River with Marion and Costello Lakes shows that Orthocladiinae are much more abundant and Chironominae less abundant in the stream than in the two lakes:

	Percent Orthocladiinae	Percent Chironominae
Bigoray River	39	39
Marion Lake	25	45
Costello Lake	14	75

Again we see the inverse relationship in the abundance of these two groups as was mentioned earlier. According to Oliver (1971), the subfamily Orthocladiinae is primarily a cold-adapted group. It is the dominant group of chironomids in the Arctic and decreases in numbers towards the tropics. Some species are known to complete their larval development below 4°C. Such cold-adapted species increase their rate of development with increasing temperatures and would be expected to be primarily multivoltine in temperate latitudes. In contrast, the subfamily Chironominae is a group of mainly thermophilous species primarily adapted to living in standing water. The number of species increases towards the tropics, and 80% of the Chironomidae living in forest streams in the Amazon region are Chironominae. At the latitude of the Bigoray River, Chironominae would be expected to be primarily univoltine. I feel, therefore, that the high percentage of multivoltine species in the Bigoray River is simply a reflection of the large number of Orthocladiinae inhabiting this northern stream.

The cold-adaptiveness of the Orthocladiinae is also apparent in several aspects of their life cycle. In my study as well as in others (Hamilton 1965, Laville 1971, Coffman (1973), the Orthocladiinae were observed to emerge primarily in spring and autumn. In the Bigoray River and Marion Lake (Hamilton 1965) larvae growing during winter belonged primarily to the Orthocladiinae.

E. Use of Emergence Traps in Chironomid Studies

The extensive use of emergence traps during this study served a number of functions. First of all, it provided a large number of male adults for species identification. Adults can also be collected by sweeping streamside vegetation with a net, but this also collects numerous terrestrial insects. Furthermore, one is never certain whether the chironomids came from the stretch of stream being studied, or from nearby bodies of water, such as the numerous burrow pits located within 100 m of the study area. It is also difficult to sweep net species which rest in tall trees. Lindegaard-Peterson (1972) collected only a few chironomids by sweeping riverside vegetation.

Many chironomid species form swarms composed primarily of males of a single species. The voluminous literature on swarming has been reviewed by Thienemann (1954), Downes (1969) and Oliver (1971). Lindeberg (1964) used swarms to obtain large samples of males known to belong to a single species. There are, however, several difficulties with this method of collecting adults. Swarms occur only during certain times of the day and may be inhibited altogether by unfavorable weather. In small species, e.g., Stempellina swarms may be composed of only a few individuals and hence be very inconspicuous. Swarming may also be absent in some species (Oliver 1971).

Another method of collecting adults is to rear the larvae in the laboratory. In my study, larval, pupal and adult stages of 41 species were associated by rearing individual larvae in small vials containing small amounts of water. Food and sediment were not placed in the vials because of subsequent difficulties in finding the larval exuviae. Although much more rearing of larvae must be done before our taxonomic knowledge of Chironomidae is complete, rearing is very time consuming and yields only a few adults. Furthermore, coloration and size of reared specimens may differ from that of specimens collected in the field (Schlee 1968).

Emergence traps enable a much more accurate determination of relative abundance of species than is possible through collection of larvae. Comparison of Tables VIII-XI with Figures 35-41 shows that the relative abundance based on emergence data can differ considerably from that based on larval collections, but, as explained on page 94, this is primarily due to the difficulty of sampling larval microhabitats in proportion to their abundance in the study area. For emergence traps to accurately reflect relative abundance of species, it is necessary that all species of chironomids exhibit surface eclosion, and that traps neither repel nor attract pupae as they rise to the water's surface. As far as is known, all species of aquatic chironomids exhibit surface eclosion (Coffman 1973). Although a number of studies have been made on the efficiencies of various emergence traps (Scott and Opdyke 1941, Guyer and Hutson 1955, Morgan et al. 1963, Macan 1964, Kimerle and Anderson 1967, Fast 1972, McCauley 1976), there is still little known about the degree to which emergence traps repel or attract insects.

My results show that opaque emergence traps catch only 33% as many chironomids as translucent traps, which transmitted 70% of the light. Kimerle and Anderson (1967) found that black box traps caught only 20% as many insects as did clear box traps. Avoidance of dark emergence traps has also been observed by Scott and Opdyke (1941) and Wohlschlag (1950). However, it remains unknown to what degree a 30% reduction in light intensity repels insects. Due to condensation inside the traps as well as build-up of dust on the traps, 70% light penetration is about the maximum that can be achieved under field conditions, even in traps with tops made of clear plastic. If one considers that most emergence occurs during the evening, it is quite likely that the slight shading has negligible effects.

Probably only chironomids that rise to the water's surface near the edge of the trap will be able to avoid the trap. In other words, if chironomids exhibit an avoidance reaction to traps, then large traps should catch more individuals per unit area than small traps, which have a greater edge effect. Indeed, Morgan et al. (1963) caught 1.4 times as many chironomids per unit area in traps covering 0.46 m^2 as in traps covering 0.37 m^2. However, even larger traps covering 0.70 m^2 caught only 65% as many chironomids as the traps covering 0.37 m^2. Similarly, McCauley (1976) could find no difference between the number of chironomids emerging inside and outside 0.1 m^2 emergence traps floating in a small swimming pool enclosed in plastic.

If emergence traps are emptied only once each week, the short-lived adults may die, fall back into the water and be washed out of the trap. This was prevented from occurring in my study by checking traps every 3-4 days. Adults dying during a sampling interval were prevented from falling out of the trap by two upturned flanges. Current velocities between 0-30 cm/sec had no effect on number of chironomids caught in the traps. Reiss (1968) found that a species of _Parachironomus_ was attracted by the unique microhabitat presented by submerged emergence traps, and therefore appeared to be much more common than it actually was. I prevented this from occurring by carefully cleaning the bottom of the emergence traps each time they were checked. In short, I feel that the emergence traps gave an accurate indication of relative abundance of chironomid species in the Bigoray River.

Emergence traps were also used to study emergence phenology of chironomid species in the Bigoray River. Emergence patterns of the four major groups were similar to those recorded by Coffman (1973) for Linesville Creek, Pennsylvania, and reflect the temperature adaptations of the groups. Orthocladiinae are the most cold-adapted group and emerge primarily in spring and autumn. Tanytarsini are also cold-adapted, but less so than Orthocladiinae, with some species being characteristic of the profundal zone of oligotrophic lakes. This would explain the emergence of Tanytarsini after the Orthocladiinae in spring, and before the Orthocladiinae in autumn. Tanypodinae and Chironomini are generally warm-adapted (Coffman 1973).

The mean emergence period of the 32 most abundant species was 64 days, slightly less than half the length of the total emergence season. The length of emergence periods varied greatly between species, from 15 days for _Diplocladius cultriger_ to 122 days for _Limnophyes_ _follicalatus_. Many factors have been shown to influence the length of emergence periods: temperature, dissolved oxygen, food competition and adaptation to past environments (Lloyd 1941, Macan 1958, Raulerson 1970, Smith and Young 1973). Abundant species might be expected to have long emergence periods to reduce intra-specific competition, while less abundant species might have short emergence periods, giving most individuals in the population a chance to reproduce. However, my data show no correlation between abundance of a species and length of its emergence period. Emergence periods occurring later on in the season were significantly longer than those occurring earlier, but this could be due to temperature or food or both.

Emergence traps also provide information on sex ratios. The mean ratio of males to females was 0.8 for the 32 most abundant species. Miller (1941) and Potter and Learner (1974) found the same average sex ratio for chironomids in Costello Lake, Ontario, and a small Welsh reservoir, respectively. Illies (1971) gives 0.9 as the average male:female ratio for chironomids in the Breitenbach, West Germany. Other examples of male:female ratios of less than one, are given by Lindeberg (1971). Like the above authors, I found that males generally emerge a few days before females. This may simply be due to the larger females requiring more degree-days to complete their development than the smaller males. Such changes in sex ratio during the emergence period can be of considerable use in separating emergence peaks of overlapping generations.

Emergence traps can be used to estimate the production of Chironomidae. This was first suggested by Illies (1971, 1972) and is based on the assumption that emergence represents a fixed proportion of the total net production of Chironomidae. Annual emergence rates have only been measured for the few aquatic systems listed below:

Locality	Number of chironomids emerging per m^2 per year
1. Breitenbach, W. Germany (Illies, 1972)	8.1×10^3
2. Rohrwiesenbach, W. Germany (Illies, 1972)	6.7×10^3
3. Kalengo, tropical stream, Zaire (Böttger, 1975)	8.9×10^3
4. Char Lake, N.W.T. (Welch, 1973)	0.6×10^3
5. George Lake, Alberta (Typha marsh) (McCauley, 1975a)	1.0×10^3
6. Kempton East Park Reservoir, 2 m England (Mundie, 1957)	6.9×10^3
7. Lake Erken, Sweden, Station M91 (Sandberg, 1969)	0.9×10^3
8. Bigoray River, Alberta (present study)	19.3×10^3

The mean annual emergence rate of chironomids in the Bigoray River is therefore over twice as high as that recorded for other bodies of water. Maximum daily emergence rates of chironomids for some bodies of water are listed below:

Locality	Maximum daily emergence of chironomids per m^2
1. Costello Lake, Ontario (Miller, 1941)	214
2. Kalengo Stream, Zaire (Böttger, 1975)	382
3. Bigoray River, Alberta (present study)	573
4. Linesville Creek, Pennsylvania (Wartinbee, 1976)	818

Again, the rates for the Bigoray River are high, being surpassed only by those for Linesville Creek. It is possible that the above figures reflect differences in methodology rather than actually differences in rates of emergence. If the differences are real, however, it is quite likely that the high rates for the Bigoray River, and probably for slow-moving streams in general, are due to abundant growth of aquatic macrophytes. These not only provide food for the larvae, but also increase the surface area ten-fold at a time when larval numbers are particularly high.

Illies (1971) found that in the Breitenbach the biomass of emerging insects alone was as high as the biomass of the whole insect community in other comparable streams. Since emergence represents only a fraction of total insect production - namely that portion which is not consumed - it indicates that past studies, based primarily on determination of the biomass of aquatic stages, have tended to underestimate production of stream insects. Although some problems are associated with emergence traps (e.g., avoidance by some insects, frequent servicing, danger of vandalism), these problems are outweighed by the many advantages of emergence traps:

1. Emergence traps provide adult males for species identification.
2. No time has to be spent sorting specimens from their substrate as is the case with bottom samples, and there are also no errors due to poor extraction techniques.
3. Emergence traps provide information on abundance, sex ratio, phenology and production.

F. Temporal and Spatial Overlap

The generally low level of temporal and spatial overlap between pairs of species, as well as the skewed shape of the overlap frequency histograms (Fig. 45, p. 123), suggest that these phenomena might result through interspecific competition. Larvae of Chironominae and most Orthocladiinae are sedentary tube dwellers. With larval densities of over 1,000/m^2 on the sediment, it is quite likely that larvae must compete with other chironomids for suitable areas on which to build their tubes. Edgar and Meadows (1969), Spence (1971) and McLachlan (1977) showed that tubes of Chironomus larvae are usually evenly spaced, and that larvae maintain a feeding territory around their tubes. Small larvae are prevented from settling in the territories of larger larvae through the aggressive behavior of the latter. At low densities, larvae occur in clumps but are evenly spaced within clumps. The clumps coalesce with increasing density, but larvae maintain their even spacing. McLachlan (1977) found that on shallow sediments the maximum density of fourth instar Chironomus larvae was 5,000/m^2 or 2 cm^2/larvae. At that density the feeding territories of adjacent larvae were touching. Cantrell and McLachlan (1977) used both field observations and laboratory experiments to show that competition for space occurs between two tube-dwelling chironomids, Chironomus plumosus and Tanytarsus gregarius. In both intra- and interspecific competition, size of larvae determines the outcome of competition. Cantrell and McLachlan were also able to obtain evidence for chironomids on four of the five criteria suggested by Reynoldson and Bellamy (1970) as being required for establishing the existence of interspecific competition.

There is, therefore, good evidence for both intra- and interspecific competition for space among chironomid larvae. Observations by other workers indicate that adults may also be competing for space in which to form swarms. Swarming of adults has been reported in many chironomids and seems to be a common and widespread behavior within the family (Thienemann 1954, Downes 1969, Oliver 1971). A swarm may be composed entirely of males or females or both, but male swarms appear to be most common. Swarms are generally composed of only a single species although multi-species swarms have been observed on rare occasions (Darby 1962, Spence 1971). Furthermore, swarms generally form in relation to specific markers such as above bushes or beneath trees (Syrjamaki 1964, Downes 1969, Spence 1971). The same species may be seen swarming over the same spot for several successive evenings. Males are attracted to the flight tones of the females. Copulation occurs the instant the male contacts the female.

Such swarming behavior probably means that each population must compete with others for suitable spaces (i.e., where the flight tones of the females are not drowned out by those of other swarms). Although the above is only speculative, detailed work on swarming by Syrjamaki (1965) and by Römer (1970) suggests that interspecific competition for swarming spaces is plausible. Such competition would explain why I found temporal overlap to remain constant throughout the emergence season, even when more species were emerging and emergence phases of individual species were becoming longer.

G. Suggestions for Future Work

This study has described the composition and the spatial and temporal structure of the chironomid community in the Bigoray River. Future work on chironomids of this stream might now proceed along one of the following lines:

1) A study of seasonal emergence patterns based on collections of pupal exuviae rather than adults would provide a check on the present results. Thienemann (1910) was the first to recommend the use of pupal exuviae since they are easily collected and do not have to be cleared prior to being mounted on slides as has to be done with larvae and adults. The use of pupal exuviae in the study of chironomid communities has increased considerably in the 1970's (Coffman 1973, Wilson and Bright 1973, Carrillo 1974, Wilson 1977, Wilson and McGill 1977). Parts of the stream could be enclosed in channels such as those used by Wartinbee (1976) and all floating pupal exuviae collected from within the channels. Since channels are completely open, they could be used to determine whether the emergence trap used in my study exhibited any shading effect.

2) A study of diel patterns of drift and emergence might indicate that temporal overlap between species is even less than indicated in my study. A study of diel emergence patterns may be incorporated with a study of pupal exuviae as was done by Coffman (1974) and Wartinbee (1978).

3) Species could be reared in the laboratory under conditions of controlled food and temperature. Determination of the day-degrees required for development, as has been done by Lloyd (1941) and Biever (1967), would provide a check on the number of generations per year as determined from field data in my study. Such rearings would also provide informa-

tion on the occurrence of larval dormancy, a phenomenon found in species of Chironomus (Fischer 1974).

4) Studies might be designed to determine the functional role of chironomids in the Bigoray River. This would involve the measurement of respiration and feeding rates of the major chironomid species as was done by Teal (1957). Studies could also be carried out in laboratory streams containing only a few chironomid species as was done by Davis and Warren (1965).

The above list could be easily extended and indicates that much still remains to be known about the chironomid community of the Bigoray River. This study has only laid the foundation, which, it is hoped, will both stimulate and assist future work.

SUMMARY

1) The 150-m study area of the Bigoray River was greatly influenced by the abundant growth of aquatic macrophytes which reached maximum standing crops of 115 gm dry weight/m^2, and increased tenfold the surface area available for colonization by benthic invertebrates. Input of terrestrial leaf litter was only one-tenth of the production of aquatic macrophytes. The upper-2 centimeters of the sediment consisted of fine to coarse sand with a varying amount of organic material. Below this was an impermeable layer of clay. Altogether, nine microhabitats could be recognized in the study area: sediment, Sparganium, Potamogeton, Hippuris, moss, filamentous algae, submerged willow leaves, submerged wood, and sponge colonies.

2) One hundred twelve species of Chironomidae were found in emergence traps in the study area. Thirty-two species had emergence rates of 50 males/m^2/yr or more, and accounted for 92% of total male emergence. Tanytarsus dispar, with an emergence rate of 1.5 x 10^3 males/m^2/yr, was the commonest species and accounted for 17% of total male emergence. More rare species were found than expected from Preston's lognormal distribution.

3) Percentage of species belonging to Tanypodinae, Orthocladiinae, Chironomini and Tanytarsini was 18%, 43%, 20% and 19% respectively. Species composition was similar

to that of other slow-flowing, lowland streams, especially the River Susa, Denmark. Percentage composition by number of individuals was: Tanypodinae 20%, Orthocladiinae 24%, Chironomini 13% and Tanytarsini 43%.

4) In 1973, emergence started May 3, when water temperature had risen to 6°C, and continued to October 1, when water temperature had decreased to 8°C. During the 4-month emergence period a total of 19.3×10^3 chironomids emerged per square meter of stream. This is the highest annual emergence rate recorded for chironomids. Maximum daily emergence rate of 573 chironomids/m^2 occurred in early August, at the time of maximum water temperature (20°C).

5) The cold-adapted Orthocladiinae had emergence peaks in the spring and autumn. The Tanytarsini, which are also somewhat cold-adapted, had a spring emergence peak which occurred just after that of the Orthocladiinae, and an autumn emergence peak occurring just before that of the Orthocladiinae. The warm-adapted Tanypodinae and Chironomini each had a single emergence peak coinciding with the period of highest water temperatures.

6) Emergence periods of individual species varied from 15-122 days, with an average of 67 days. In ten of the 32 commonest species, emergence rates varied unimodally with time (i.e., emergence period consisted of a single "emergence phase"). In 15 species emergence rates varied bimodally (i.e., two emergence phases), and in 6 species it varied trimodally (i.e., three emergence phases). Only Nanocladius sp.n. 1

showed no distinct emergence phases. Instead, this species emerged in dribbles throughout the emergence period. In species with two phases, 44% of the individuals emerged during the first phase and 56% during the second phase. In species with three phases, the percent of individuals emerging during the first, second and third phases was 31%, 20% and 49%, respectively.

7) The ratio of males to females was 0.8 for the total sample of adult chironomids. The ratio was significantly less than 1.0 in 14 of the 32 commonest species, and more than 1.0 for two of the 32 commonest species. Males emerged a few days ahead of the females, so that the ratio of males to females decreased steadily throughout an emergence phase.

8) Of the 32 species examined, 11 (34%) were univoltine, 15 (47%) were bivoltine, and six (19%) were trivoltine. The warm-adapted Chironomini were primarily univoltine, while the cold-adapted Orthocladiinae had the highest percentage of trivoltine species. All of the species overwintered as larvae: 19% in the 2nd instar, 16% in the 2nd and 3rd instars, 44% in the 3rd instar, 12% in the 3rd and 4th instars, and 9% in the 4th instar. Winter growth of larvae appeared to be restricted to Orthocladiinae and Tanytarsini.

9) Density of larvae on bottom sediment varied from $3.1 \times 10^3/m$ to $52.9 \times 10^3/m^2$ during the 23-month study period, with a mean density of 19.9×10^3 larvae/m^2. Minimum densities occurred in June and maximum densities in March.

Average densities of larvae on Sparganium, Potamogeton, Hippuris, moss, filamentous algae and sponge were 93, 171, 466, 978, 351 and 32 larvae/gm dry weight of the respective substrates. Mean density of wood was 0.9 larvae/cm^2. Low larval densities on the sediment during summer resulted from emergence of adults and migration of larvae onto aquatic macrophytes. Decomposition of macrophytes during winter causes larvae to move back onto the sediment, and this accounts for increase in larval density on the sediment during winter.

10) Preferred habitat of Tanypodinae and Chironomini was sediment. Orthocladiinae preferred Sparganium, moss and filamentous algae, and Tanytarsini preferred Potamogeton. Twenty of the 32 commonest species occurred either exclusively or predominantly in only one of the nine microhabitats, 11 predominated in either two or three microhabitats, and only Paramerina fragilis was a habitat generalist. Cricotopus sp. n., a species preferring filamentous algae, exhibited the highest degree of habitat specialization.

11) Average overlap of emergence periods among the 32 commonest species was 24%, while the average overlap of larvae among the nine microhabitats was 37%. The low average overlap values and the skewed shape of overlap frequency histograms suggest interspecific competition for space by larvae and adults. Interspecific competition for space among chironomid larvae has been documented by other workers. Interspecific competition for swarming spaces among adults is sug-

gested by the swarming behavior as described in the literature, and by my observation that the overlap of emergence periods of species did not increase during the emergence season, even though the number of species emerging and the length of emergence phases increased with time. Spatial overlap was much higher on the sediment than in the other eight microhabitats, and indicates that larvae subdivide the sediment into a number of microhabitats, possibly based on one or more of the following parameters: particle size, organic content, compaction, or species composition and abundance of the benthic microorganisms. Temporal and spatial overlap between congeneric species was higher than between non-congeneric species. Temporal and spatial overlap was also higher between species belonging to different trophic levels than between species belonging to the same trophic level. This was probably due to the association of predators with their prey. Pairs of species with high temporal overlap also tended to have high spatial overlap.

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